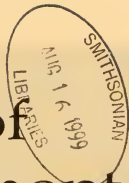




Journal of Hymenoptera Research



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CONTENTS

MESSAGE FROM THE PRESIDENT	1
PHYLOGENY SYMPOSIUM	
DEDICATION	2
ALEXANDER, B.A. An exploratory analysis of cladistic relationships within the superfamily Apoidea, with special reference to sphecoid wasps (Hymenoptera)	25
CAMERON, S.A., J.N. DERR, A.D. AUSTIN, J.B. WOOLLEY and R.A. WHARTON. The application of nucleotide sequence data to phylogeny of the Hymenoptera: a review	63
SHARKEY, M.J. and D.B. WAHL. Cladistics of the Ichneumonoidea (Hymenoptera).	15
WHITFIELD, J.B. Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera	3
INVITED PAPERS	
AESCHLIMANN, J.P. AND R.D. HUGHES. Collecting <i>Aphelinus</i> spp. (Hymenoptera: Aphelinidae) in southwestern CIS for "pre-emptive" biological control of <i>Diuraphis noxia</i> (Homoptera: Aphididae) in Australia	103
BOHART, R.M. The genus <i>Oxybelus</i> in Chile (Hymenoptera: Sphecidae, Crabroninae)	157
BROTHERS, D.J. The first Mesozoic Vespidae (Hymenoptera) from the Southern Hemisphere, Botswana ...	119
GESS, F.W. A new southern African species of the genus <i>Celonites</i> Latreille (Hymenoptera: Vespidae, Masarinae) associated with the flowers of <i>Wahlenbergia</i> (Campanulaceae)	141
GESS, F.W. and S.K. GESS. Ethology of three southern African ground nesting Masarinae, two <i>Celonites</i> species and a silk-spinning <i>Quartinia</i> species, with a discussion of nesting by the subfamily as a whole (Hymenoptera: Vespidae)	145
GRISSELL, E.E. A revision of <i>Perissocentrus</i> Crawford (Hymenoptera: Torymidae)	91
KIMSEY, L.S. Functional morphology of the abdomen and phylogeny of chrysidid wasps (Hymenoptera: Chrysididae)	165
KURCZEWSKI, F.E., M.F. O'BRIEN, and M.G. SPOFFORD. Nesting behavior of <i>Podalonia robusta</i> (Cresson) (Hymenoptera: Sphecidae)	235

(Continued on back cover)

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Message from the President

In December, 1982 at the Entomological Society of America meetings in Toronto, Canada, a large group of hymenopterists met to discuss formation of an organization devoted to the study of all aspects of the Hymenoptera. From that embryonic meeting emerged The International Society of Hymenopterists with nearly 300 members and still growing as this message was being prepared. During the early stages of development of the Society we had many discussions about the pros and cons of establishing a journal. Finally, in 1990 an editorial board, composed of Arnold Menke, John Huber, Mark Shaw and David Rosen, was elected to search for an editor and begin the process of starting the new journal, and in 1991 David Smith was selected as editor. You have in your hands the results of this effort, the inaugural issue of the *Journal of Hymenoptera Research*.

We hope this first issue will set the tone for the *JHR* as a major outlet for reporting research on the Hymenoptera in all their glory. This first issue is composed of invited papers from researchers around the world as well as a few papers from the phylogeny symposium presented at the Society meetings held in Sheffield, England, August 1991. The quality of presentations and diversity of subjects represents a fine beginning for this new journal and I hope it will encourage more members to submit manuscripts for future issues. Editor Smith already has a few manuscripts for the next issue with others expected, so we are off to a good start.

This first issue could not have been realized without the time and efforts of several people. On behalf of the Society, I wish to thank the Editorial Committee and in particular Arnold Menke for selecting an outstanding editor, for inviting an excellent group of authors and subjects for the first issue, and for helping in the establishment of guidelines for the future. Dave Smith has spent many hours searching for a printer, preparing the instructions for authors, and finalizing the style for the journal, for which we offer our thanks. I am also very grateful for the following people who offered financial assistance to help get this issue on its way:

FOUNDERS (\$1000)

Richard M. Bohart
Karl V. Krombein

PATRONS (\$500)

Franco Borgato

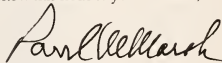
BENEFACTORS (\$100)

E. Eric Grissell
Joong-Suk Park

In addition there were numerous **Sustaining Members (\$50)** as well as those who included donations along with their dues. To all these generous people, we could not have done it without you!

During the last year we had a contest to create a Society logo. The winning design was submitted by Michael Prentice, University of California, Berkeley, who also designed the cover page for the journal. Congratulations and thanks to Mike.

Finally, I encourage all members to use the *JHR* to reach the masses with their important research findings. Where else can you find a bargain of no page charges in the US! Also, please show this issue to your libraries; we need to establish more subscriptions to support the journal.



Paul M. Marsh
President

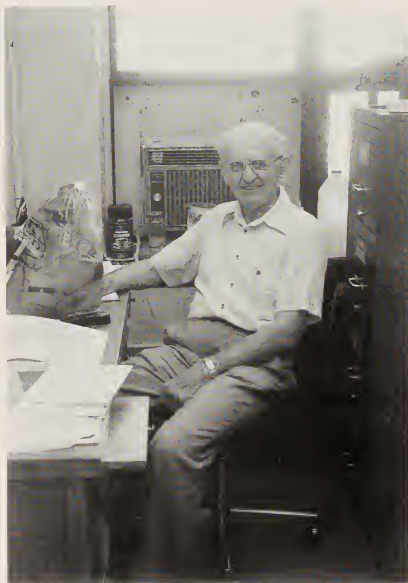
Phylogeny of Hymenoptera

DEDICATION

The first four articles in this issue are selected papers presented in a symposium "Phylogeny of Hymenoptera" at the Second Quadrennial Meeting, Sheffield, U.K., August 11-17, 1991.

As the papers from this symposium were going to press, we were saddened to learn of the death of W.R.M. (Bill) Mason during the last days of 1991. Bill was one of the prime movers in studies of Hymenoptera phylogeny during the last two decades, and his as yet unpublished studies of comparative mesosomatic and metasomatic skeletomusculature and the evidence it provides for phylogenetic analysis of Hymenoptera were well known to many of us through papers read at meetings as well as informal discussions with him.

Bill's interest in Hymenoptera spanned many years and covered many groups beyond his usual specialities of Braconidae and Ichneumonidae. He will be greatly missed not only for his regular contributions to hymenopteran phylogeny and classification, but also for his cheerful and open approach to criticism and scientific debate. This first, one hopes, of many collections of papers on hymenopteran phylogeny to be featured in this journal, is dedicated to him.



W.R.M. Mason, August 1990, in his office at the Biosystematics Research Centre, Ottawa

Phylogeny of the Non-Aculeate Apocrita and the Evolution of Parasitism in the Hymenoptera

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Abstract.— Recent interest in the higher-level phylogeny of Apocrita has led to the advancement of several competing hypotheses of relationships among major lineages. Nevertheless, some areas of agreement do exist among these hypotheses, providing a base from which further progress can be made. A well-corroborated phylogeny for the Apocrita would be extremely useful for interpreting the evolution of parasitism, among other features, within the Hymenoptera. Comparative studies of parasitoid/host biology are still at a relatively early stage. Most of what is known of parasitoid biology is derived from relatively few taxa of Ichneumonidea, Chalcidoidea and Scelionidea, and even within these groups data are extremely sparse. A number of specialized biological features associated with endoparasitoid groups show intriguing patterns of distribution among taxa, but so little is known of these features across all taxa that coherent evolutionary hypotheses concerning these features cannot yet be advanced. It is suggested that more emphasis be given to *comparative parasitoid biology*, especially within poorly-known groups.

Interest in the evolution of the Hymenoptera is certainly not new; broad treatments of the phylogeny of the order and the evolution of the food habits of its members span at least most of this century (e.g. Handlirsch 1907, Börner 1919, Bradley 1958, Malyshev 1968, Iwata 1976, Tobias 1976, Hennig 1981). Only within the past several decades, however, have relatively explicit and practical methods of phylogenetic inference been available so that studies of hymenopteran evolution have become repeatable and open to productive criticism. Even more recent is the wholesale recognition of the value of specific phylogenetic hypotheses for interpreting the evolution of biological traits (e.g. Coddington 1988, Donoghue 1989, Brooks and MacLennan 1991, Harvey and Pagel 1991).

Although this by no means implies that studies of hymenopteran evolution prior to the last few years do not continue to be valuable (such careful studies as those of Oeser 1961 and Brothers 1975 on Aculeata, for instance, have held up remarkably well to further scrutiny), it is much easier to evaluate the more recent ones in the light of the actual evidence that is presented, so that one study builds upon another.

In this brief overview I first hope to quickly cover some of the major findings and controversies of recent phylogenetic studies of the higher taxa of

Hymenoptera, focusing especially on the non-aculeate Apocrita, which were often under-represented and poorly understood in earlier studies. I will begin with the exhaustive literature review and analysis of Königsmann (1976, 1977, 1978a,b) and continue to the present, attempting to consolidate some areas of agreement among the various studies and to point out where disagreement is rampant and further study would be most valuable.

In the second main segment of this paper I briefly review what is currently known about various comparative aspects of the parasitoid habit among the groups of non-aculeate Apocrita. I will first focus on the ways in which parasitoids have overcome the problems associated with an evolutionary transition from ectoparasitism (the putative ancestral form of parasitic lifestyle in Hymenoptera) to endoparasitism. There will follow a brief discussion of how some of these parasitoid "strategies" are distributed among hymenopteran higher taxa. Although an attempt will be made to illustrate the value of a phylogenetic perspective in interpreting such comparative data, the major goal of this review is to point out areas where new comparative biological data would add appreciably to our understanding of the evolution of parasitism in the Hymenoptera. It is one major virtue of a phylogenetic approach that the distribution and depth of comparative data among taxa must be made explicit so that areas of ignorance become clear.

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RECENT PHYLOGENETIC STUDIES OF APOCRITA

Königsmann (1976, 1977, 1978a,b) compiled a large, predominantly morphological, data set from the literature, for phylogenetic analysis of higher-level relationships within the entire order Hymenoptera. His analyses, although rigorous and based on the largest data set produced to that time for hymenopteran phylogeny, suffered from the lack of sufficient characters for many groups, partly because he did not contribute new ones but also because the data set did not include a number of characters already evident to other workers for various groups. Nevertheless, his study did represent perhaps the first rigorous attempt to analyze relationships within the order, and served to highlight the lack of knowledge of, and lack of resolution among, most of the non-aculeate apocritan groups. Figure 1 represents his findings for the Apocrita in an abbreviated form. It is of some significance that his data appear not to support the monophyly of any non-aculeate apocritan groupings above the superfamily level (other than the somewhat controversial one of Evanioidea + (Cynipoidea + Chalcidoidea)), nor of the monophyly of the traditional Proctotrupoidea. Masner and Dessart (1967) had already suggested that the Ceraphronoidea should be recognized as a separate superfamily, but the inability of the available data to support the monophyly of the remaining taxa was somewhat surprising. In addition, Königsmann's analyses suggested that the extant sister-group to Apocrita was most likely the Cephoidea, as Malyshev (1968), among others, had suggested.

The next major set of contributions to apocritan phylogeny were made by Rasnitsyn (his papers of 1980 and 1988 are most relevant to the present discussion). In addition to a more thorough knowledge of comparative morphology across many groups, Rasnitsyn's work included comprehensive consideration of the available fossil evidence, much of which had rarely been examined by workers outside of the USSR. Although the details of his phylogenetic hypotheses and classifications evolved somewhat over the years, his 1988 paper largely summarizes the others and provides a concise introduction to the evidence he uses to support his phylogeny. A simplified version of his cladogram of the Apocrita (redrawn and omitting extinct taxa) is provided in Figure 2; Figures 3 and

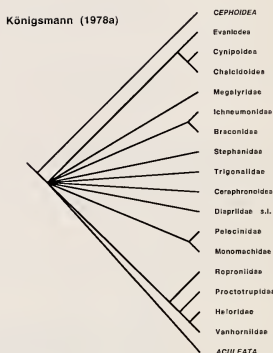


Fig. 1. Cladogram of non-aculeate Apocrita modified from Königsmann (1978a). Note especially the almost complete lack of resolution among the basal branching in the suborder.

4 represent his phylogenetic views on subsets of taxa from Figure 1.

Rasnitsyn's (1980, 1988) cladogram was the first comprehensive, essentially fully resolved phylogenetic hypothesis for the non-aculeate Apocrita that utilized the principle of grouping on the basis of shared derived features. He produced some radical changes in the higher classification of Hymenoptera, several of which are still controversial. His classification suffers from two major weaknesses: 1) his philosophy of classification allows phenetic distinctness to override the strict phylogenetic branching sequences, so that paraphyletic groups are preserved if distinct enough from monophyletic sub-assemblages, and 2) he did not make use of automated searches for most parsimonious trees, so that alternative explanations of the data were often not considered. Nevertheless, his work marked a major progressive step in the study of hymenopteran phylogeny. To a large extent, most subsequent studies have focused on

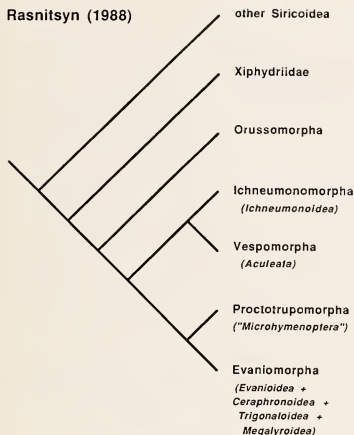


Fig. 2. Cladogram of major lineages of non-aculeate Apocrita greatly modified from Rasnitsyn (1988). Fossil taxa have been deleted from this representation of his work, and several putative monophyletic groups have been collapsed into single units. Figures 3 and 4 are more detailed treatments of parts of this figure.

testing his ideas and, to date, no comprehensive study has yet superseded his.

Rasnitsyn (1980, 1988) established clearly that the extant sister group to the traditional Apocrita is the Orussidae, a relationship that virtually all subsequent studies (e.g. Gibson 1985, Johnson 1988; Whitfield et al. 1989) have confirmed and that provides a direct biological link between the Symphyta and the parasitoid habit among the Apocrita. Secondly, he proposed two large groupings below the level of suborder that were not previously recognized: the Proctotrupomorpha (Fig. 3 - Chalcidoidea + Proctotrupoidea s.l. + Cynipoidea + Scelionoidea) and the Evaniomorpha (Fig. 4 - Evanioidea + Ceraphronoidea + Trigonalioidea + Megalyridae + Stephanidae). His Ichneumonomorpha corresponded to the traditional Ichneumonoidea and the Aculeata, as recognized by Oeser (1961) and Brothers (1975), remained with its usual boundaries. Of his novel findings, the Evanioidea is the most controversial grouping, in particular the inclusion within it of Stephanidae and Trigonalioidea. Al-

though some relationships within this proposed higher taxon have been supported by subsequent studies (Johnson 1988), morphological evidence now suggests (Gibson 1985, Johnson 1988, Mason, unpublished) that the Stephanidae occupy an extremely basal position within the Apocrita and are not closely related to the other "Evaniomorpha". The Proctotrupomorpha grouping has been supported in large measure by the comparative skeletomusculature studies of W.R.M. Mason (unpublished, there treated as the "Microhymenoptera").

Although no single study has superseded that of Rasnitsyn (1980, 1988), the accumulation of additional comparative morphological studies along the lines of Gibson (1985, 1986) on thoracic skeletomusculature, Johnson (1988) on mesothoracic skeletomusculature and midcoxal articulations, Robertson (1968) on venom apparatus, Darling (1988) on the labrum, Whitfield et al. (1989) on the metapostnotum and associated musculature, and the ongoing studies by W.R.M. Mason (in preparation, featuring especially the mesosomal-metasomal articulation and musculature) will clearly be helpful in further resolving higher relationships within

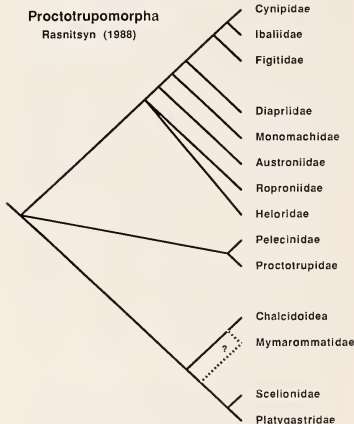


Fig. 3. Rasnitsyn's (1988) hypothesis of relationships among the "Proctotrupomorpha". The uncertain relationship of Mymaromatidae (but see Gibson 1986) is denoted by dotted lines; otherwise, lack of resolution is indicated by polytomies.

the Apocrita, as will molecular systematic studies now still in their early stages (see elsewhere this issue). Care must be taken, however, to include many of the less easily available taxa, such as Megalyridae, Stephanidae, Trigonalidae and Orussidae, since these have proven to be critical taxa in determining the larger phylogenetic patterns especially in the early evolution of Apocrita.

HYMENOPTERA AS PARASITOIDS

If the Orussidae are the sister-group to the Apocrita, as is presently best supported by the available evidence, the parasitoid habit may have had a single, unique origin within the Hymenoptera—in the common ancestor of Orussidae and Apocrita. The biology of orussids is poorly studied, but what is known is consistent with ectoparasitism of xylophagous Coleoptera, with the egg laid near the (possibly envenomated) host (Cooper 1953, Powell and Turner 1975, Gauld and Bolton 1988). This biology is remarkably similar to that of basal lineages of Ichneumonoidea, Evanioidea (albeit at least some Aulacidae are apparently endoparasitoids), Stephanidae and Megalyridae. It is also not terribly different in the host/parasitoid relationship to that of basal groups of Aculeata.

Some sort of ectoparasitic habit, therefore, appears to be a groundplan state for many (but not all—note the apparent absence of any extant ectoparasitoids among the Cynipoidea, Scelionoidea and Proctotrupeoidea *s.l.*) of the major apocritan lineages. Although many variations of behavior and host-parasitoid interaction do exist among ectoparasitoids, and these are of considerable phylogenetic interest as well, it is among the endoparasitoids that the most extreme elaborations of parasitoid habits have been developed. I would like to focus on what currently can be postulated of the evolution of these various forms of endoparasitism, based on what is known of comparative parasitoid biology, and what is known, or hypothesized, of the phylogeny of the Apocrita. But first a brief discussion of what it means to be a hymenopteran endoparasitoid.

THE PROBLEMS OF ENDOPARASITISM

It has been apparent for some time that the condition called "endoparasitism" is really a collection of different biological relationships, all of which share the feature of the parasitoid feeding from entirely inside the host organism, rather than from the outside.

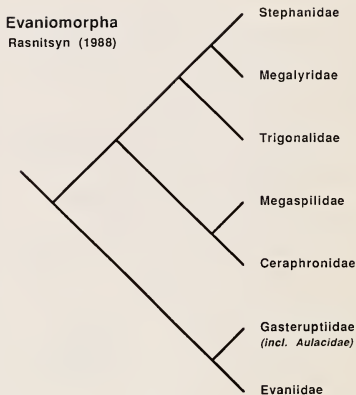


Fig. 4. Rasnitsyn's (1988) hypothesis of relationships among the "Evaniomorpha". Note his inclusion of Trigonalidae and Stephanidae in this assemblage.

Many of the features usually associated with endoparasitism are actually associated more closely with koinobiosis (Askew and Shaw, 1986; Gauld, 1988; Gauld and Bolton, 1988). This refers to a prolonged, complex interaction with the host (and in endoparasitoids this is with the internal milieu of the host), in contrast to the rapid feeding on moribund hosts more often found in ectoparasitoids (idiobiosis). Some of the most physiologically complex interspecific interactions known to science are between endoparasitic koinobionts and their host organisms, and many of the details of even the best-known cases are not fully elucidated.

There are major evolutionary problems to be solved in any transition from ecto- to endoparasitism, or from idiobiosis to koinobiosis. The defense reactions of the host insects, especially the cellular responses (Götz 1986, Lackie 1980, Nappi 1975, Salt 1968, 1970) must be overcome once the transition is made to development within host organisms. The parasitoid may have to control the physiology of the host to some extent (Beckage 1985, Jones 1985, Lawrence 1986, Stoltz 1986, Vinson and Iwantsch 1980b), or it must prevent the hormonal milieu of

the host from controlling its own physiology, or at least use the host's physiological signals to its own advantage (Lawrence 1986, Jones 1985).

The solutions to these problems in endoparasitoids appear to have varied greatly from group to group, depending on the options open to them during their evolutionary history. In a few cases the parasitoid may be able to avoid some of the above problems by placing its egg in particular host tissues, or by insulating itself in some way. In at least one species of *Eretmocerus* (Chalcidoidea), the parasitoid larva, although technically an endoparasitoid, is encased within a capsule that protects it from the internal milieu of the host (Gerling et al. 1990). In most cases, however, more direct interaction with the host is encountered, and parasitoids have a number of "tools" at their disposal for dealing with this interaction. For instance, many ectoparasitoids use a *venom* to temporarily or permanently paralyze the host (Beard 1978, Piek and Spanjer 1986, Steiner 1986). The evolution of this paralytic venom is an interesting problem in itself. Even phytophagous Siricoidea and Cephoidea secrete compounds (whether homologous or not) that influence either the host plant or fungal associates of the host plant in ways that benefit the developing wasp larva. How the first paralytic venoms might have arisen from any such possible precursors is not known, as comparative biochemical analyses of venoms and associated substances are still in their early stages. The neurotoxic and preservative effects of the paralytic venoms of parasitoids are of considerable pharmaceutical interest, but have not yet been capitalized upon. There are some chemical similarities between some components of these venoms and components of the more well-studied venoms of the social Hymenoptera (for a review of comparative aspects, see Piek 1986 and Leluk et al. 1989), as should be expected since the ancestral biology of Aculeata is ectoparasitism.

In endoparasitoids the venom may retain a paralyzing function, or be adapted to influence the host physiology in some way, or act in both ways, or neither (Shaw 1981, Piek and Spanjer 1986, Steiner 1986, Stoltz 1986). Leluk et al. (1989) have shown that the venom of many endoparasitoids contains large protein components not found in the paralytic venoms of ectoparasitic Apocrita. In addition, a number of interactions between venoms and other parasitoid-derived products have been reported (Stoltz 1986, Stoltz et al. 1988, Tanaka and Vinson

1991a,b), so that the extent of host modification or regulation that can be directly attributed to venom is relatively poorly known, and for only a few taxa. The problem is clearly a complex one, but future surveys of venom components from groups in which the phylogenetic relationships and host/parasitoid biologies are known may suggest functions for some of the venom proteins and aid in the understanding of the biochemical aspects of host/parasitoid interactions (Leluk et al. 1989). In this respect, comparative systematic studies of venom gland structure, as begun by Edson and Vinson (1979) and Edson et al. (1982) may also provide initial insights into venom functions even before biochemical analyses are undertaken.

In many braconids and assorted other parasitic Hymenoptera (see below), the serosa or trophamnion associated with the parasitoid egg appears to facilitate the uptake of nutrients by the developing embryo, and may fragment into individual free-floating cells variously called teratocytes (Salt 1968, Vinson 1970, Vinson and Iwantsch 1980b, Dahlman 1990) or "giant cells" (Jackson 1935, Gerling and Orion 1973), among other names. That some kind of nutritive function is served by these teratocytes has been suspected by many workers, but other functions attributed to them, such as production of juvenile hormone (Vinson 1970, Joiner et al. 1973) or fungicidal activity (Führer et al. 1978), dissolution of host tissues (Mackauer 1959, Sluss 1968, Gerling and Orion 1973) or overwhelming of the host's cellular defenses (Salt 1968, 1970), are less well established and require much further investigation (Vinson and Iwantsch 1980b, Stoltz 1986). However, at least the juvenilizing effects are being corroborated by recent work (Strand and Wong 1991). It is not clear that "teratocytes" are a homologous phenomenon in all of the parasitoids studied; much further comparative morphological and developmental work is required. An additional complication for such studies will be that in some species, teratocytes may be diversifying into different types with age (Strand and Wong, 1991).

In some endoparasitoids, *viruses* associated with the adult female wasps are injected with the eggs, either aided or not by venom effects. These viruses can effectively suppress the immune system of the host as well as cause some other physiological changes (Rotherham 1967, Stoltz and Vinson 1979, Faulkner 1982, Beckage 1985, Blissard et al. 1986, Stoltz 1986, Guzo and Stoltz 1987, Jones 1987, Dover et al. 1987, 1988, Schmidt and Theopold, 1991).

Recent studies indicate that at least some of these viruses are integrated into the wasp genomes and are inherited from mother to offspring (Stoltz et al. 1986, Fleming and Summers 1986, Stoltz 1990). The predominant group of viruses that has been studied are the polydnaviruses, of two rather distinct (and probably distantly, if at all, related) types associated with some subfamilies of Ichneumonidae and Braconidae, respectively. Other kinds of viruses are known to be associated with parasitoid ovaries or venom glands, however, and may be of greater significance than is currently realized (Edson 1981, Stoltz 1981, Lawrence and Akin 1990, Rizki and Rizki 1990). A more comprehensive overview of the associations between parasitoids and viruses is presented elsewhere in this issue (Stoltz and Whitfield 1992). Inheritance (strictly vertical transmission) suggests that at least some virus strains and their relationships should correlate with the phylogenies of the wasps themselves, providing an example of how knowledge of the phylogenetic relationships of the parasitoids can guide lines of productive research in other areas. It should be possible, using modern molecular genetic techniques and co-phylogenetic approaches (e.g., Page 1990, 1991, Brooks and McLennan 1991) to investigate the coevolution between the wasps and viruses and their evolutionary interactions with host organisms. Some initial efforts are already being made along these lines (Cook and Stoltz 1983, Whitfield 1990, Stolz and Whitfield 1992).

Host/parasitoid physiological interactions are quite complicated syndromes of behaviors and phenomena (Fisher 1971, Vinson and Iwantsch 1980a, 1980b, Jones 1985, Lawrence 1986, Strand and Wong 1991, Thompson 1983, 1990) that might also be found to show phylogenetic trends, independent of whether the precise "tools" the parasitoids and hosts use to effect them can be elaborated. Variations occur in whether host ecdysis and development from one instar to another are possible, and in whether the parasitoid larva uses host hormonal levels to time its own development (Beckage 1985, Lawrence 1983, Shaw 1983). Parasitoid groups might be found to have general requirements for survival that can be satisfied in different specific ways depending on the host group being attacked. Whether any given interactive endocrine response is selectively advantageous in its current situation or whether it has been inherited as a part of a syndrome from distant ancestors (or both) is seldom known, but could perhaps be ap-

proached with additional comparative data. Integration of phylogenetic relationships of parasitoids with information gleaned from representative study organisms should help to clarify the evolutionary significance of many of these host/parasitoid endocrine interactions. However, one major caveat should be added about the use of phylogenetics in interpreting the evolution of complex biological habits. The success of any phylogenetic study depends not only upon the accuracy of the biological information put into it, but also upon the sensible division of the often complex biological features into independent, unitary character states. In this respect, detailed comparative studies of the biologies of related organisms, such as those done by Shaw (1983) and Whitfield (in press), may prove a crucial step in the elucidation of more complex evolutionary sequences.

Relatively little can be said definitively about the evolution of various parasitoid habits among the Hymenoptera until more well-defined phylogenetic relationships are known and considerably more comparative biological data is available. However, I attempt below to briefly touch upon what patterns can be seen by reviewing of the literature on apocritan parasitoids, focusing particularly on the distributions of venom types, viruses and teratocytes among endoparasitoids. It will quickly become obvious that few conclusions should be drawn from the information presently available. Nevertheless, the exercise may be useful in suggesting areas where further information is especially needed.

PHYLOGENETIC TRENDS IN HOST/PARASITOID BIOLOGY

It has been remarked upon above that the groundplan biology for many of the apocritan lineages is a form of ectoparasitism marked by oviposition on or near a partially or totally incapacitated host, usually in a concealed situation. For each infraorder discussed below, I will briefly touch upon the extent to which this groundplan biology is still found in the group, and in what major ways divergence has occurred from this groundplan within the group. Repeated reference to Table 1, which shows the distribution (if known) among taxa of a persistent trophamnion, teratocytes and/or viruses that may affect the host, may be useful as a quick reference for endoparasitoid taxa when some aspects of host/parasitoid biology are being

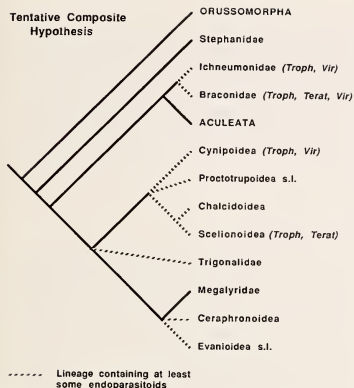


Fig. 5. Composite hypothesis of apocritan relationships, based largely on Rasnitsyn (1988) but modified based upon findings by Mason (unpublished), Gibson (1985), Johnson (1988) and Whitfield et al. (1989). Lineages marked as containing endoparasitoids may also contain (often among their basal clades) some ectoparasitoids. **Troph** - presence of a persistent trophamnion, at least through first instar, in at least some species. **Terat** - presence of some sort of teratocytes in at least some species. **Vir** - presence of some sort of associated viruses (that are introduced into host insects) in at least some species. Not all species in lineages marked with these abbreviations necessarily, nor are all occurrences of a trophamnion, teratocytes or viruses assumed to be homologous. Apparent absence of a trophamnion, teratocytes, or viruses in a lineage may be simply due to lack of data in many cases. Both the tree and the distribution are offered to suggest groups in which further research would be especially helpful.

discussed. Figure 5 shows the phylogenetic distribution of the presence of these features, as superimposed upon a "composite cladogram" concocted from the hypothesis of Rasnitsyn (1988) combined with refinements by other concurrent and subsequent research (e.g. Mason unpublished, Gibson 1985, 1986, Johnson 1988, Whitfield et al. 1989).

"Ichneumonomorpha"

The ectoparasitoids found within basal lineages of both Ichneumonidae and Braconidae appear to fit the general groundplan biology in possessing paralyzing venoms for incapacitating hosts (the

venom of *Bracon* being the best-studied example - see Beard 1978 and Piek 1986 for more details) and rapid development of the larvae upon the usually moribund host. Within each of these two families some form of endoparasitoid habit has appeared several times (see Gauld 1988 for overview; Shaw 1983 and Whitfield, in press, provide a relatively well-studied example from the Braconidae). Within each of the two families a number of derived features associated with endoparasitism have independently appeared in remarkably similar fashion - a prominent case being the existence of mutualistic viruses associated with immune suppression of hosts in microgastrinae and chelonine and related braconids and in campoplegine and a few other ichneumonids. There is no real indication, however, that the ichneumonid-associated viruses and the braconid-associated viruses are particularly closely related, let alone form a monophyletic group.

Gauld (1988) has pointed out some differences between the two families in evolutionary trends in parasitism, especially in the host groups exploited and in what way they are utilized. An additional difference that appears from a review of the literature is that many braconids possess teratocytes that influence the host/parasitoid relationship, whereas these are not known from Ichneumonidae. Nevertheless, I expect that this trend will be found to hold only at some level lower than the family level, since teratocytes appear to be absent from many endoparasitoid braconids and few ichneumonids have been intensively studied enough to rule out the existence of teratocytes during their development.

In both families, but particularly in Ichneumonidae, some endoparasitoids of host pupae are found that apparently do not interact in a particularly active or long-term way with the host and show little biological similarity to the more derived larval endoparasitoids, as Gauld (1988) has pointed out. In this respect they are similar to the egg parasitoids found in other superfamilies.

Despite the large gaps in our knowledge of comparative biology of Ichneumonoidea, this group is certainly biologically the best-known of major non-aculeate apocritan groups, at least in terms of the intimate details of host-parasitoid biology. Nevertheless, much of what is known has been studied in only a few taxa, e.g. Microgastrinae, Aphidiinae and Campopleginae.

"Proctotrupomorpha"

Within this infraorder true ectoparasitoids are found, to my knowledge, only within some groups of Chalcidoidea (especially some or many Chalcididae, Eurytomidae, Torymidae, Eupelmidae, Pteromalidae, Eulophidae and Elasmidae). A number of other groups within Chalcidoidea and Scelionoidea parasitize insect eggs and are not particularly highly derived in their adaptation to endoparasitism, although a few unique venom-associated substances and functions are known (Strand 1986). Nevertheless, the diversity in host/parasitoid biology within this infraorder is truly incredible, ranging from ecto- to endoparasitism, solitary to gregarious and polyembryonic development, spanning a highly diverse array of host organisms; it is difficult to generalize about trends in the evolution of parasitism. Even within some large families such as Pteromalidae, Eulophidae and Encyrtidae, the diversity of lifestyles is bewildering. Although some detailed comparative work has been undertaken on egg parasitoids (especially *Trichogramma* and Scelionidae - e.g., see Strand 1986 and Strand and Wong 1991 for some comparative review), the twin difficulties of poorly known biology (at least at the level of detailed host/parasitoid interactions) and still unsatisfactory (but very rapidly improving) classification for many groups of "Proctotrupomorpha" have hindered comparative work. The potential for significant study of the evolution of parasitism in this infraorder is enormous.

A few generalizations can be made. Many of the ectoparasitoids within the Chalcidoidea appear to possess paralyzing venoms and exhibit rapid development within the host organism, as is the general plesiomorphic rule for apocritans. Some of the less derived endoparasitoids, such as the Ibalidae in the Cynipoidea, appear to possess a final ectoparasitic feeding phase, which might be relatively plesiomorphic, as has been suspected in some braconid groups (Shaw and Huddleston 1991). Within the Chalcidoidea, Proctotrupoidea s.l. and Platygastriidae some spectacular larval developmental modifications have evolved, the functions of which are not always understood, but appear to be characteristic of phylogenetic lineages. In general, the Proctotrupoidea as a group appear to be relatively less derived in their methods of endoparasitism, but details of their host/parasitoid interactions are sketchy. The equally, if not

even more, poorly-understood parasitic Cynipoidea sporadically exhibit some unusual features, such as mutualistic viruses analogous to those of Ichneumonidae (Rizki and Rizki 1990), but too little is known of most species to generalize in any significant way about them. Table 1 provides some indication of how little we know currently of some aspects of proctotrupomorph host/parasitoid biology.

"Evaniomorpha"

As discussed above, recent research indicates that this infraorder from Rasnitsyn's (1988) classification is probably not a monophyletic group. Hence, there is perhaps little reason to suspect it to have any biological coherence, even when it is better known biologically. Whatever similarities the Stephanidae and Megalyridae might have, for instance, in ectoparasitism of concealed xylophagous insects, are probably ancestral states shared with many other basal lineages of Apocrita.

The only true endoparasitoids found within this group are within the Trigonalyidae, Ceraphronidae (but not the Megaspilidae) of the Ceraphronoidea, and the Aulacidae of the (possibly also not monophyletic) Evanioidea. The details of the host/parasitoid interaction in these endoparasitoid groups is extremely poorly known and they appear to have little in common with one another biologically. Other groups, such as the Evaniidae and Gasteruptionidae, are hardly parasitoids at all, the former perhaps being better described as predators of cockroach eggs and the latter as consumers of solitary bee larval provisions (and sometimes also of bee larvae). It is possible that the largely hyperparasitic biology of the Trigonalyidae (reviewed by Weinstein and Austin 1991) could ease the difficulties of development of endoparasitoid life in this group, in that they often attack hosts whose immune systems have already been compromised by other parasitoids. No really complex host/parasitoid physiological phenomena have been described in this complex of Hymenoptera, but so little is known that the discovery of such phenomena would not be surprising.

FUTURE RESEARCH

The above brief survey of apocritan parasitoid biology is not a complete review of the subject. The interested reader is referred instead to the more

Table 1. Taxonomic distribution of some "tools" used by endoparasitoids in interactions with host insects. Refer to text for further explanation (especially for those portions of the table where question marks appear). Although space does not permit an exhaustive listing of supportive references here, most sources of information are cited in the text; where essentially nothing is known, a "?" appears; where conflicting or inconclusive reports are available, a "+?" or "-?" appears.

	Trophamnion	Teratocytes	Viruses
<i>Ichneumonomorpha</i>			
Ichneumonidae	+	-	+
Braconidae	+	+	+
<i>Proctotrupomorpha</i>			
Cynipoidea	+	-	+
"Proctotrupeoidea"	-	-	-
Chalcidoidea	-?	-?	-?
Scelionoidea	+	+	-?
<i>Evaniomorpha</i>			
Megalyroidea	-	-	-
Trigonidae	?	-	-?
Ceraphronoidea	-?	-?	-?
Evanioidea	-	-	-

comprehensive treatments of Clausen (1940), Askew (1971), Fisher (1971), Vinson and Iwantsch 1980a,b, Thompson (1983), Beckage (1985), Lawrence (1986), Slansky (1986), Stoltz (1986), Gauld and Bolton (1988), Coudron (1990) and Thompson (1990). This review is offered more as a stimulant to further comparative work on parasitoid biology, using the phylogeny of the groups, as far as is known, as a guide. I hope to have demonstrated some areas and groups where further information is most needed, but there really are no biologically well-known higher taxa represented here. Recent developments in physiology, molecular genetics, immunology, cell culture and many other areas now make some aspects of comparative parasitoid biology approachable for the first time. The potential of the parasitic Hymenoptera, both as biological systems for the study of parasitism and as subjects of evolutionary research, has still barely been tapped, relative to the wealth of information that lies yet undiscovered.

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Cladistics of the Ichneumonoidea (Hymenoptera)

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Abstract.—We recognize only two extant families, Ichneumonidae and Braconidae, in the Ichneumonoidea. All other recent taxa that have been regarded as family-level taxa can be reasonably placed within one or the other family. We find no evidence to place Praeichneumonidae in the Ichneumonoidea and therefore consider it *incertae sedis* in the Apocrita. Likewise, though it is an ichneumonoid, there are no synapomorphies which suggest that *Tanychora* is an ichneumonid. The cladograms of fossil and recent ichneumonoids support the monophyly of Eoichneumonidae and a sister-group relationship with Braconidae.

The purpose of this paper is to review and revise the family-level cladistics and classification of the Ichneumonoidea. The families comprising the Ichneumonoidea have fluctuated considerably over the years and recent classifications have included from two to seven extant families, i.e., from only Braconidae and Ichneumonidae, (e.g., Gauld and Bolton, 1988) to various combinations of the following: Agriotypidae (e.g., Mason 1971); Aphidiidae (e.g., Tobias 1989; Mackauer 1968; Mackauer and Stary 1967; Stary 1966; Conca 1973); Apozygidae, (Mason 1978); Braconidae; Ichneumonidae; Megalyridae (Pagliano and Scaramozzino, 1990); and Paxylommatidae (e.g., Achterberg 1976a; Mason 1981). We examine the validity of these familial concepts from a cladistic perspective and recognize a classification that consists of only two families, Braconidae and Ichneumonidae.

PLACEMENT OF THE ICHNEUMONOIDEA WITHIN HYMENOPTERA

Rasnitsyn (1988) suggested that Aculeata (his Vespomorpha) is the sister-group of Ichneumonoidea on the basis of the shared possession of an apomorphic condition of the propodeal foramen and the presence of valvelli in the ovipositor (Gauld 1976; originally referred to as hemmplättchen by Oeser 1961). The propodeal foramen, into which the metasoma is inserted (Fig. 1), is narrow and subdivided by a pair of tooth-like condyli (the "propodeal teeth").

Zessin (1985) suggested that the Ichneumonoidea is the sister-group of the remaining Apocrita. He based the monophyly of the Apocrita exclusive of the Ichneumonoidea on the loss of the anal veins, 2A and a, of the fore wing. In Zessin's phraseology, all traces of the lanceolate cell (anal) are lost. Within the Apocrita, traces of the lanceolate cell, in the form of 2A and crossvein a, are found only in some Braconidae. Although he did note that the veins must be convergently lost in the Ichneumonidae and the 'remainder of the Apocrita', Zessin did not consider the fact that they could be a reversal, an equally parsimonious interpretation.

A third hypothesis was presented by Rasnitsyn (1980) and supported by Johnson (1988). This is that Ichneumonoidea, Chalcidoidea, Cynipoidea, and Proctotrupoidea s.l. (excluding Cerafronoidea) are a monophyletic group, the Ichneumonomorpha. Johnson supported the Ichneumonomorpha on the basis of the apomorphic condition of the midcoxal articulations, i.e., a reduced basicoxite, a deep coxal groove, and laterally displaced coxal cavities. According to Johnson, an identical character occurs in several lineages of Aculeata. A total of six steps accounts for the distribution of the character, with one derivation in Ichneumonomorpha, and four derivations and one reversal in Aculeata. If, however, one considers the Ichneumonoidea to be the sister-group of the Aculeata, the number of steps is the same for a clade consisting of Ichneumonoidea, Aculeata, Cynipoidea, Chalcidoidea, and Proctotrupoidea (using the

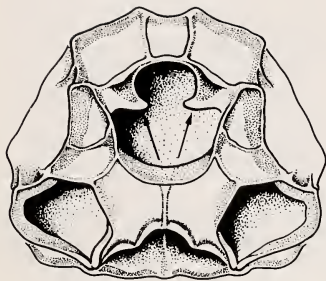


Fig. 1. *Alabagrus texanus*, posterior view of mesosoma with legs and metasoma removed. Arrow indicates the propodeal teeth in the propodeal foramen.

cladogram of Aculeate family relationships given in Johnson's figure 35).

Taking all the evidence into consideration, i.e. coxal articulations, wing venation, valvilli, and propodeal teeth, the sister-group relationship with the Aculeata is the most parsimonious hypothesis.

MONOPHYLY OF THE ICHNEUMONOIDEA

Character polarity for our cladistic analysis (Maddison et al., 1984) was based on the following sequential ordering of outgroups: Aculeata, other Apocrita, Orussidae, Xiphydriidae, other Symphyta (Gibson 1985, Rasnitsyn 1988). It is based on the distribution of character states in these outgroups that we suggest the following autapomorphies for the Ichneumonoidea.

1. Adult mandible with two teeth (Mason 1987). The plesiomorphic condition is three or perhaps four mandibular teeth, as in almost all Symphyta, and the vast majority of Apocrita. Some derived lineages of Chalcidoidea, Cynipoidea, Proctotrupoidea, and Scelionoidea have two teeth, but based on our surveys the ground plan of all of these taxa appears to be three or more teeth. Within the Ichneumonoidea, the teeth have been reduced to one in some lineages. In Alysiinae, and some Opiinae the number has been increased to three or four. In Ichneumonidae the upper tooth has become

subdivided in Diplazontinae and certain Banchini.

2. Prepectus fused to posterior lateral (vertical) margin of the pronotum, mesothoracic spiracle positioned directly above prepectus, and external pit indicating origin of spiracular occlusor muscle lying near posterior pronotal margin (Gibson, 1985).

3. Sternum of first metasomal segment divided into heavily sclerotized anterior section and comparatively weakly sclerotized posterior section (Mason 1981, 1987). This character is found only in Ichneumonoidea.

4. Metasomal segments 1 and 2 articulated by a pair of dorsolateral condyles on the hind margin of tergum 1 and anterior margin of tergum 2. This character is found only in Ichneumonoidea (Mason 1987). The plesiomorphic condition is that metasomal segments 1 and 2 do not articulate on dorsolateral condyles so that they can telescope; such telescoping is not possible in ichneumonoids. In some other Apocrita this telescoping ability may be lost due to partial or complete fusion.

5. Costa and radius of fore wing adjacent/appressed, such that the width of the costal cell is narrower than the costal vein (Fig. 2). In many ichneumonoid taxa the costal cell is completely absent. Convergent appearances of this character are found in other Apocrita, most notably Rhopalosomatidae and miscellaneous Larridae.

6. Vein 2r-m of fore wing absent. The identity of the veins making up the apparent r-m cross veins of the fore wing has been a matter of some dispute. One interpretation is described by Tobias and Belokobylski (1984), with Braconidae possessing 2-Rs and 2r-m (3r-m is lost) and Ichneumonidae possessing 2r-m and 3r-m (2-Rs is lost). Much of the argument of the these authors was based upon instances of aberrant venation in braconids. Rasnitsyn (1980) was of the opinion that 2r-m was lost (2-Rs and 3r-m retained) in an ancestral ichneumonoid and we have adopted this interpretation as it best accounts for venation in fossil taxa. For example, in the Cretaceous ichneumonoid *Tanychora* (Fig. 3) the outermost r-m crossvein is well distad 2m-cu, the usual position for 3r-m in Hymenoptera, and 2-Rs is in the plesiomorphic basal position. In the instances of 2m-cu occurring in braconids cited by Tobias and Belokobylski (Fig. 4), the outermost vein is in the same position. Rather than posit a migration of 2r-m from its usual position between 1m-cu and 2m-cu, Rasnitsyn's suggestion seems simpler. Rs is therefore considered to have migrated apically in

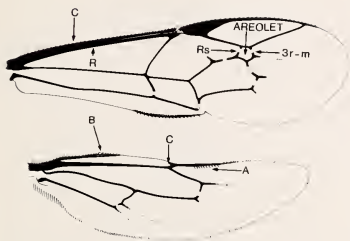
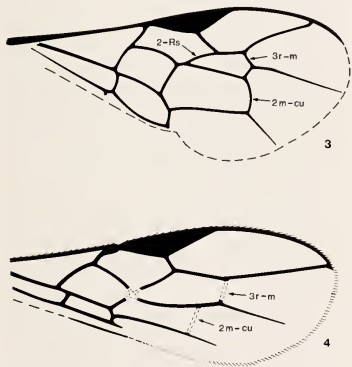


Fig. 2. Ichneumonidae sp., fore and hind wing. B = basal hamuli, A = apical hamuli C = costa



Figs. 3, 4. 3, *Tanychora petiolata*, fore wing, 4, *Ontsira rara*, fore wing.

Ichneumonidae to form the family's characteristic areolet (Fig. 2).

7. Larva with hypostomal spur. Ichneumonoid larvae possess an extensive system of sclerotized bands around the mouthparts. The hypostoma is a sclerotized band running posteriorly along the subgenal margin of the cranium; a spur projects ventrally from the hypostoma across the stipes (Fig. 5). The hypostomal spur is found only in

Ichneumonoidea and apparently functions to help brace the labium during cocoon construction. It has been lost on several occasions in braconids and ichneumonids, usually in taxa that do not spin cocoons (Short, 1978).

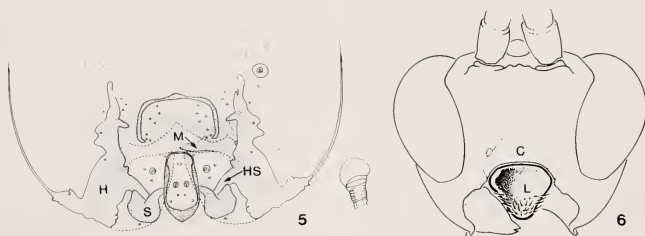
TAXA THAT HAVE BEEN RECOGNIZED AS FAMILIES OF ICHNEUMONOIDEA

Agriotypus

This group is usually recognized as an ichneumonid subfamily by ichneumonid researchers e.g., Townes (1969). *Agriotypus* shares the two known autapomorphies of Ichneumonidae, the apical displacement of vein 2-Rs of the fore wing with the resulting formation of the characteristic ichneumonid areolet, and loss of vein 1-Rs+M of the fore wing. We keep *Agriotypus* within Ichneumonidae.

Aphidiinae

It is now fairly well accepted that Aphidiinae are derived braconids sharing all of the braconid synapomorphies (detailed below). The character that has caused some confusion in the group's placement is the presence of an apparent suture between metasomal terga 2 and 3. When examined carefully, this is found to be a weakness in the fused terga rather than a true suture. Therefore, the braconid synapomorphy of fused terga 2 and 3 is valid even with the inclusion of Aphidiinae. Some specialists, particularly Tobias (1968, 1989) and Tobias and Starý (in the 1988 edition of the newsletter *Ichnews*) maintain that Aphidiinae should have familial status. Tobias (1989) stated that there are two well established lineages within the Braconidae, the cyclostomes (Apozyginae, Alysiinae, Braconinae, Doryctinae, Gnampodontinae, Opiinae and Rogadinae s.l.) and the clade of endoparasitoids representing all other braconids. To date there has been no compelling evidence to associate the Aphidiinae with either of these lineages, and on the basis of this negative evidence, Tobias (1968, 1989) argued that Aphidiinae should be considered the sister-group of the braconids. In our view, this is faulty logic. If, as Tobias and Starý appear to believe, the cyclostome braconids, the Aphidiinae and the non-cyclostome braconids form an unresolved trichotomy, the Aphidiinae could represent the sister-group of either or both of the two other taxa. There are synapomorphies defining the Braconidae



Figs. 5-6. 5, *Grotea* sp., head capsule. H = hypostoma, HS = hypostomal spur, M = mandible, S = stipital sclerite. 6, *Aleiodes terminalis*, head. C = clypeus, L = labrum

including the Aphidiinae, but when one excludes the Aphidiinae there is none. This is sufficient reason to classify the Aphidiinae within the Braconidae.

Apozyx

Apozyx is represented by one species known only from Chile. Mason (1978) described the species and proposed family rank in the Ichneumonidae. It has also been included as a subfamily of the Braconidae (e.g., Quicke and Achterberg, 1990)

Apozyx shares all four synapomorphies of the Braconidae, i.e., migration of vein 1r-m to or basal to the separation of veins R1 and Rs in the hind wing, loss of functional basal hamuli, loss of stub of vein C of the hind wing basad the distal hamuli, and fusion of metasomal terga 2 and 3.

In our view, *Apozyx* is a cyclostome braconid. The most telling synapomorphy supporting this hypothesis is that the labrum is the typical cyclostome type: concave, triangular, smooth, and mostly glabrous (cf. Fig. 6) and the ventral margin of the clypeus is concave (Fig. 6).

Apozyx may be the sister-group of the remaining cyclostomes, all of which have lost the second abscissa of vein Cu (2-Cu) of the hind wing (Fig. 8). The only character which argues against this placement is the apparently plesiomorphic presence of vein 2m-cu in the fore wing of *Apozyx* (Fig. 8). This vein is present in the Ichneumonidae and other outgroups but present in no other Braconidae except some freak specimens, e.g. *Ontsira rara* (Fig. 4) (Tobias and Belokobylskij, 1984). It is more parsimonious to hypothesize a recurrence of 2m-cu in *Apozyx* than treat the cyclostome characters as convergences.

Braconidae (including Aphidiinae and *Apozyx*)

This is one of the two families we recognize in Ichneumonidae. The family is supported by four autapomorphies.

The first autapomorphy, the fusion of metasomal terga 2 and 3, is found without exception in all known braconids. It is also found convergently in derived lineages of Ichneumonidae and Aculeata, but, based on its distribution within these taxa, the plesiomorphic condition of mutually articulating terga must be considered to be part of the ichneumonoid and aculeate ground plan.

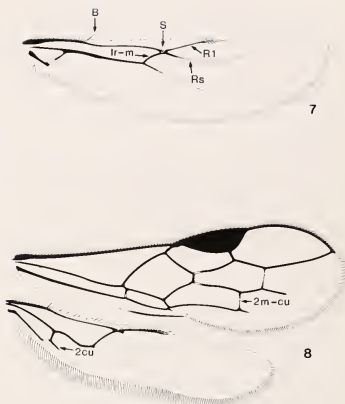
The second autapomorphy is the loss of functional basal hamuli on vein C of the hind wing. Functional basal hamuli are hooked and are found near the point where veins C and R of the hind wing diverge (Fig. 2). Basal hamuli are found in some members of the Braconidae, e.g., Braconinae (Fig. 7), but they do not form hooks and do not appear to function as wing couplers. Functional basal hamuli are widespread in Ichneumonidae (Fig. 2), Aculeata, Trigonalidae and the symphytan superfamilies, but are unknown in the Braconidae. It is worth noting here that the convergent loss of functional basal hamuli in the Apocrita exclusive of the Ichneumonidae, Aculeata and Trigonalidae, may be a synapomorphy for this assemblage. This suggestion is supported by several venational characters such as the loss of the second closed Rs cell in the fore wing and the loss of a closed Cu cell in the hind wing.

A third autapomorphy of Braconidae is the loss of an independent stub of vein C of the hind wing, basad the distal hamuli (Fig. 7). Vein C is complete in some Aculeata and presumably the ground plan for the group (Brothers, 1975). Many aculeate taxa have some indication of vein C basad the point

where R or R1 meets the anterior wing margin. Although vein C of the hind wing is incomplete in all Ichneumonidae, most Ichneumonidae have retained a small stub of vein C basad the point where R1 meets the anterior margin (Fig. 2) and this is the most parsimonious assignment for the ground plan.

The fourth braconid autapomorphy is the basal migration of vein 1r-m of the hind wing, to or basal to the separation of veins R1 and Rs (Fig. 7); the plesiomorphic condition is for 1r-m to be apical to the separation. Ichneumonidae, Aculeata, other Apocrita, e.g. Trigonalidae, and most Symphyta have this plesiomorphic state. In at least one ichneumonid taxon (*Neorhacodes*) 1r-m is opposite the R1-Rs separation, but never basad. There are several braconid taxa such as *Trachypetys* and *Rhamphobarcon* where reversals have occurred.

Mason (1981) discussed the various positions of the r-m crossveins in ichneumonoids. He posited the ancestral ichneumonoid to have two r-m crossveins with Ichneumonidae having lost 1r-m and Braconidae having lost 2r-m. We reject Mason's arguments because explicit outgroup analysis exposes them as unsupported. With rather convincing support, Gibson (1985) postulated the following pattern of relationships: (Siricidae (Xiphydriidae (Orussidae + Apocrita))). We are unaware of any Apocrita with two r-m crossveins, with the exception of some braconids. Furthermore, the one crossvein present in apocritans is always opposite or distad the point of separation of R1 and Rs, with the aforementioned exception of braconids (Gauld, 1984). Orussids have only one crossvein, which is distad of the separation by about the length of the crossvein. Xiphydriids have three crossveins: r-m and 3r-m are tubular, 2r-m is spectral. It is noteworthy that 1r-m is well distad of the R1 and Rs separation and in the same position as the 1r-m crossvein of ichneumonids and aculeates. There are two r-m crossveins in the siricid hind wing; the most basal varies from basad to distad the separation, and the outermost one is in the position of 3r-m of xiphydriids and the Jurassic siricoid *Protosirex* (Mason, 1981: Fig. 5). No trace of a crossvein can be seen between the two existing crossveins. We therefore conclude that the most parsimonious solution to the question of hind wing r-m homologies is to consider: (1) 2r-m and 3r-m to be lost in the common ancestor of Apocrita + Orussidae, (2) 1r-m to be shifted in braconids to a position basad the separation of R1 and Rs, and (3) the second r-m crossvein of some braconid



Figs. 7-8. 7, *Coeloides rufovariegatum*, hind wing. B = basal hamuli, S = elongate setae. 8, *Apozyx penyai*, fore and hind wing.

subfamilies to be the product of one or more reversals. The preceding hypothesis prevents the wildly unparsimonious scenario of multiple 2r-m losses.

Ichneumonidae (including *Agriotypus* and *Paxylommatinae*)

Ichneumonids are usually recognized by having 1-Rs+M absent and metasomal terga 2 and 3 articulating. The former character is apomorphic though it is also found in widely scattered groups of braconids; the latter is plesiomorphic. What other apomorphies distinguish the family? Mason believed that ichneumonids lack 1r-m in the hind wing; our objections to that hypothesis are detailed above in the discussion of Braconidae. Tobias and Belokobylski (1984) argued that the areolet in braconids and ichneumonids is formed by different veins (2-Rs and 2r-m in braconids, 2r-m and 3r-m in ichneumonids). Again, our objections to that idea are presented in the section dealing with ichneumonoid autapomorphies. Ichneumonidae have a very characteristic, small, areolet (Fig. 2). If our hypotheses on fore wing vein homologies are correct, then the apical displacement of vein 2-Rs is

necessary to account for the small areolet. A precursor condition to this may be the long and slanting vein 2-Rs of *Tanychora* (Fig. 3), but this is quite speculative. In summary, we put forward the loss of fore wing vein 1-Rs+M, and the apical displacement of fore wing vein 2-Rs as autapomorphies of the Ichneumonidae.

Megalyridae

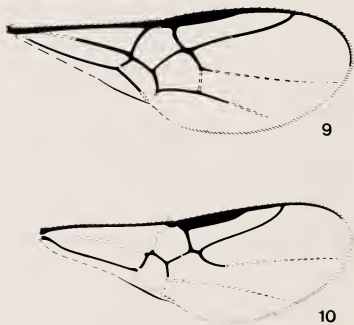
Pagliano and Scaramozzino (1990) include this family in the Ichneumonoidea in their catalog of hymenopteran generic names. This is a rather novel hypothesis which we reject since megalyrids lack the ichneumonoid synapomorphies discussed previously.

Paxylommatinae

This taxon consists of two extant genera, *Hybrizon* Fallén and *Ghilaromma* Tobias. Paxylommatinae has been treated as a subfamily of Braconidae (Shenefelt 1969; Achterberg 1976a,b), a separate family (Tobias 1968; Marsh 1971, 1979; Mason 1981; Achterberg 1984), and a subfamily of Ichneumonidae (Rasnitsyn 1980; Gauld 1984; Gauld and Bolton, 1988).

Paxylommatinae has been placed in the Braconidae on the basis of the absence of vein 2m-cu in the fore wing. The large number of autapomorphies has led to its recognition as an independent family. Mason (1981) was the first to examine *Hybrizon*'s relationship to Ichneumonidae and Braconidae from a phylogenetic perspective. He demonstrated that metasomal terga 2 and 3 are not fused, thus excluding *Hybrizon* from the Braconidae. Further evidence of this is that 2m-cu of the fore wing appears to be part of the paxylommatine ground plan, as demonstrated by the fossil paxylommatine *Tobiasites striatus* from Baltic amber (Fig. 9) (Kasparyan 1988). On the basis of his ideas on hind wing r-m homologies, Mason (1981) suggested that the r-m crossvein of *Hybrizon* is 1r-m and eliminated the genus from membership in the Ichneumonidae. As discussed earlier under the section on Ichneumonidae, we reject this interpretation.

Achterberg (1984) hypothesized Paxylommatinae to be the sister-group of Ichneumonidae, citing as evidence the absence of vein 1-Rs+M in the fore wing, and loss of vein 1r-m in the hind wing. In turn, this assemblage was considered to be the sister-group of Braconidae. We agree that Paxylommatinae and Ichneumonidae are closely related, although we disagree with the interpretation of hind wing venation for reasons



Figs. 9–10. 9, *Tobiasites striatus*, fore wing. 10, *Hybrizon flavocinctum*, fore wing.

presented above. Achterberg gives four autapomorphies supporting the monophyly of Paxylommatinae but only one character for Ichneumonidae exclusive of Paxylommatinae — the presence of an accessory longitudinal tracheal commissure. This may be a good autapomorphy for ichneumonids, although more taxa need to be surveyed. The main criticism of his use of the character is that the larval stages of members of Paxylommatinae have never been described. How can one differentiate between two groups when the critical character for one of them is unknown? Achterberg's argument for the sister-group relationship of Paxylommatinae and Ichneumonidae appears unsupported.

Members of Paxylommatinae (Fig. 10) lack vein 1-Rs+M, as do all ichneumonids. At present, this is the strongest direct evidence placing it in the Ichneumonidae although the reliability of the character is somewhat vitiated by its multiple losses in Braconidae. As mentioned earlier, Rasnitsyn pointed out the similarity of *Hybrizon*'s venation to that of *Neorhacodes*. Members of both genera parasitize aculeate Hymenoptera, and they may well be sister-groups.

Stephanidae

The Stephanidae have often been included within Ichneumonoidea (Townes 1969; Carlson 1979). Townes (1969) based the superfamily Ichneumonoidea on: a) distinct vein C of the fore wing, b) veins C and R of the fore wing adjacent or

fused so there is no costal cell between them, c) antenna with more than 14 flagellomeres, and d) adult mandible with two teeth.

We reject these arguments for the following reasons. Vein C is absent in Stephanidae, and even if it were present the presence of vein C is plesiomorphic. Contrary to ichneumonoids, stephanids possess a narrow but distinct costal cell anterad vein R. The polarity of the character state, antenna with more than 14 flagellomeres, is uncertain and quite possibly plesiomorphic. Finally, stephanid adults have only one apical mandibular tooth not two. Within the context of the characters analyzed here, the propodeal teeth and valvilli discussed in section one are absent in stephanids and they possess only one of the ichneumonoid apomorphies discussed earlier, the loss of vein 2r-m of the fore wing. This convergent loss is found in all of the larger apocritan lineages and therefore is not particularly convincing. Thus, there appears to be little evidence to support the placement of the Stephanidae in the Ichneumonoidea.

FOSSIL ICHNEUMONOIDEA

Rasnitsyn (1983) described *Praeichneumon townesi* as a new family (Praeichneumonidae) in Ichneumonoidea; the specimen is from Lower Cretaceous deposits in Mongolia. Placement in the Ichneumonoidea was based on a narrow costal cell of the fore wing, an external ovipositor, and an antenna with more than 13 flagellomeres (Rasnitsyn 1983; Rasnitsyn and Sharkey 1988). Examination of Rasnitsyn's figures (Rasnitsyn, *ibid.*) reveals a distinct costal cell, unlike the condition in other ichneumonoids where the costal cell is narrower than the costal vein. An external ovipositor is a plesiomorphic character state for the Apocrita and of no value for determining relationships at this level of investigation. Numerous flagellomeres might be a ground plan character state for the Apocrita because it is present in several taxa that appear to be basal in the Apocrita based on characters such as venation, e.g., Trigonalidae, Stephanidae. Finally, *Praeichneumon* has vein 2r-m present in the fore wing, a vein that all ichneumonoids have lost (see above discussion). The lack of the critical ichneumonoid synapomorphies listed at the beginning of this essay leads us to remove this species from Ichneumonoidea and consider it *incertae sedis* within the Apocrita.

Several other fossil Hymenoptera are of interest. Townes (1973) described *Tanychora* from the lower Cretaceous of Transbaikalia. He placed it in the Ichneumonidae, stating that the genus could be "ancestral to all of the modern Ichneumonidae, it could represent an extinct phyletic line, or it could be a primitive representative of 1 of the modern subfamilies. There is not sufficient evidence to eliminate any of these 3 possibilities." Rasnitsyn (1980) placed *Tanychora* in its own subfamily (Tanychorinae) in the Ichneumonidae.

Eoichneumon was described from a specimen of the early Cretaceous of Australia (Jell and Duncan 1986) and the family Eoichneumonidae was proposed for the genus. Rasnitsyn and Sharkey (1988) described an additional three genera and 14 species (*Baissobracon* (1 species), *Cretobraconus* (7 species), *Archobraconus* (6 species)) in Eoichneumonidae. These species are from the early Cretaceous of Siberia and Mongolia.

The above fossil genera were defined by combinations of plesiomorphic and apomorphic characters, and hence their status and relationships are uncertain. We have compiled a data matrix using Townes (1973) and Rasnitsyn and Sharkey (1988) as sources of characters. The set of available characters is quite small since few characters are visible in fossil impressions. Ovipositor length and length of 1-Rs of the fore wing were used by Rasnitsyn and Sharkey, but these characters are not employed here because of their variable nature, lack of polarity, and our inability to code the ground-plan for the Ichneumonidae and Braconidae.

The characters, polarized using the same outgroups as those used to support the monophyly of the Ichneumonoidea, are as follows; the data matrix is given in Table 1.

1. Fore wing vein 1-Rs+M
0: present
1: absent.
2. Fore wing vein 1cu-a
0: apical vein 1-M
1: basal vein 1-M.
3. Fore wing vein 2-Rs
0: basal position (basal apex of stigma)
1: apical position (apical apex of stigma).
4. Fore wing vein 3r-m
0: tubular
1: spectral/absent.
5. Fore wing vein 2m-cu.
0: tubular
1: spectral/absent.
6. Hind wing vein 1r-m.
0: apical separation of veins Rs and R1

- 1: at or basal to separation of Rs and R1. (The hind wing is missing in *Eoichneumon*.)
7. Notauli of mesoscutum.
0: separated for their entire length
1: converging before scutellum. (The mesoscutal surface cannot be seen in *Baissobracon*.)
8. Surface of propodeum.
0: areolate
1: finely reticulate.
9. Metasomal terga 2-3.
0: articulated
1: fused.
10. Metasomal terga 1-2.
0: without prominent longitudinal striae.
1: with prominent longitudinal striae.

The relationships among Ichneumonidae, Braconidae, *Tanychora*, *Eoichneumon*, *Baissobracon*, *Cretobraconus*, and *Archobraconus* were analyzed using the Hennig86 cladistics program (version 1.5) of Farris (1988). The ie (implicit enumeration) option resulted in four cladograms. One of the cladograms was supported only by an ambiguous optimization and was rejected (Platnick et al. 1991). The remaining cladograms (Fig. 11) had a length of 11 steps, a consistency index of 0.83 (excluding autapomorphies), and a retention index of 0.85. Some characters used in the analysis, especially loss or weakness in veins, may be difficult to determine in fossil specimens due to poor preservation or variable impression. Therefore, some of the conclusions that follow, particularly those concerning the monophyly of the Eoichneumonidae, are rather speculative.

Our conclusions are: 1) The cladograms support the monophyly of the Eoichneumonidae based on the reduction or absence of fore wing crossvein 3r-m. 2) The clade Eoichneumonidae plus Braconidae is supported by the loss or reduction of fore wing crossvein 2m-cu. 3) The inclusion of *Tanychora* in the Ichneumonidae or any other family may not be inferred from the data and therefore we consider it as a plesion in the Ichneumonoidea.

Wiley (1981) discusses the problems of classifying fossil taxa of uncertain placement, using the convention of *incertae sedis* and the plesion concept. Wiley defines the latter (p. 205), modified from the original concept of Patterson and Rosen (1977), as "a name of variable rank accorded a fossil species . . . when classified with one or more Recent species or groups." Wiley goes on to say (p. 219) that "the use of 'plesion' is a conservative means of classifying fossils with Recent taxa . . . no matter how many times the plesion's phylogenetic position may change in relation to its Recent relatives."

Table 1. Data set of extinct and extant ichneumonoid taxa (characters described in the text).

Taxa	Characters									
	1	2	3	4	5	6	7	8	9	10
outgroup	0	0	0	0	0	0	0	0	0	0
Ichneumonidae	1	0	1	0	0	0	0	0	0	0
<i>Tanychora</i>	0	0	0	0	0	0	0	0	0	0
<i>Baissobracon</i>	0	1	0	1	1	0	?	1	0	1
<i>Cretobraconus</i>	0	0	0	1	1	0	0	1	0	0
<i>Eoichneumon</i>	0	0	0	1	1	?	0	0	0	0
<i>Archobraconus</i>	0	0	0	1	1	1	1	0	0	0
Braconidae	0	0	0	0	1	1	0	0	1	0

Thus, applying Wiley's sequencing convention, a classification of extant and fossil taxa that are considered Ichneumonoidea is as follows:

Superfamily Ichneumonoidea *incertae sedis*:

- Plesion *Tanychora*
- Family Ichneumonidae
- Family Braconidae
- Family Eoichneumonidae

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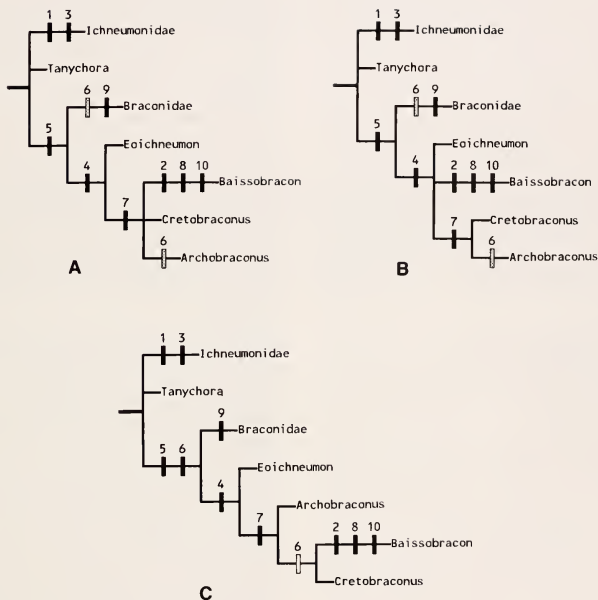


Fig. 11. A-C are the three minimum length cladograms from the data set of extinct and recent ichneumonoid taxa (Table 1), character descriptions are presented in the text. Black bars = apomorphies, grey bars = parallelisms, white bars = reversals

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An Exploratory Analysis of Cladistic Relationships within the Superfamily Apoidea, with Special Reference to Sphecid Wasps (Hymenoptera)^{1,2}

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Abstract.—This paper presents the results of several analyses of cladistic relationships among the sphecid wasps and bees, based on adult and larval morphology, with special emphasis on the tribes of sphecid wasps. The analyses examine the effects of: (1) alternative procedures for determining character polarities, (2) using adult characters alone or both adult and larval characters, (3) analyzing all sphecid tribes or only those tribes for which larvae have been described, and (4) equal weighting of all characters vs. successive approximations character weighting. The monophyly of bees is strongly supported, and the following groups of tribes of sphecid wasps are consistently supported as monophyletic: (a) Ampulicini + Dolichurini; (b) (Sceliphriini + (Sphecini + Ammophilini)); (c) (Aphilanthopini + Philanthini + Cercerini + Pseudoscoliini); (d) (Nyssonini + Gorytini + Stizini + Bembicini). Numerous equally parsimonious resolutions of cladistic relationships among these groups and other sphecid tribes are found.

In 1976, R. M. Bohart and A. S. Menke published a monumental worldwide revision of the genera of sphecid wasps. This encyclopedic compilation of information on the taxonomy, geographic distribution, and external morphology and behavior of adults represents a milestone in our knowledge of these wasps. Another noteworthy feature of this work is its extensive discussions of phylogenetic relationships among sphecid wasps, although its numerous phylogenetic diagrams are not based upon explicitly stated analytical methods. However, Bohart and Menke (1976: Tables 2, 5, 11, 13, 15, 16, 19, and p. 224) present numerous lists of "generalized" and "specialized" states of characters considered to be "of phylogenetic significance" in various groups (usually subfamilies). The implicit message seems to be that the branching diagrams are based upon the characters in these tables. Regardless of how the phylogenetic diagrams may have been derived, the character analyses summarized in the tables do provide the kind of information necessary for a cladistic analysis. Thus, it seems in principle be possible to determine how well these characters support the phylogenetic hypotheses presented by Bohart and Menke, and whether there are other phylogenetic hypotheses that would explain the data equally well or better.

A rigorous cladistic analysis requires two types of information in addition to that presented in Bohart and Menke's tables of character states. One is a clear statement of how the characters have been polarized, and the other is a matrix showing the state of each character for each taxon. Bohart and Menke do not present any data matrix in their book, and it is not possible to construct a complete matrix from their descriptions of taxa or discussions of characters. In one of their introductory chapters (p. 29), they do briefly explain how they distinguished between "primitive" and "advanced" states of characters. After discussing the pitfalls of assuming that "simple" characters are primitive and "complex" ones derived, they conclude that "a study of features common in the more primitive hymenopterous families and preserved in some of the Sphecidae is the most productive way of making value judgments on evolutionary paths". This is conceptually close to a method now generally known as outgroup analysis, although more recent formulations of this method (e.g. Watrous and Wheeler 1981, Maddison et al. 1984) are considerably more rigorous and explicit. Bohart and Menke also do not identify which hymenopteran families they consider primitive (relative to sphecid wasps). The first explicit cladistic analysis of aculeate Hymenoptera (Brothers 1975; not cited in Bohart and Menke 1976) presented a hypothesis of the phylogenetic position of sphecid wasps and bees that was quite different from conventional opinion at the time (e.g. Evans and West Eberhard 1970).

¹ Contribution No. 3033, University of Kansas

² Throughout this paper, the informal designation "sphecid wasps" will be used to refer to all taxa assigned to the Family Sphecidae as defined by Bohart and Menke (1976).

Thus, it is not at all certain that the families regarded as primitive by Bohart and Menke would be those selected now in the light of new hypotheses of phylogenetic relationships among aculeate families that have resulted from explicit cladistic analyses (Brothers 1975, Königsman 1978, Carpenter 1990).

Another important and influential source of information and ideas about sphecids phylogeny has been presented by H.E. Evans and colleagues, in a series of papers describing sphecids larvae and analysing larval characters from a phylogenetic perspective (Evans 1957b, 1958, 1959, 1964a, 1964b, 1966, Evans and Lin 1956a, 1956b, Evans and Matthews 1968). Evans has found larval characters to be most phylogenetically informative for groups that he treats as subfamilies (see especially Evans 1959, 1964). The number of characters employed in his analyses is considerably less than the number of adult characters presented in Bohart and Menke's tables, but a few noteworthy larval characters seem to provide evidence of general patterns of higher-level relationships. The way in which Evans presents and analyzes data on larval characters is very similar to the approach adopted by Bohart and Menke, and the same general remarks on the limitations of this approach apply to both data sets.

The potential importance of larval characters for elucidating higher level phylogenetic relationships among sphecids wasps was recently re-emphasized in a cladistic analysis of the relationships between sphecids wasps and bees published by Lomholdt (1982). He partitions the paraphyletic Sphecidae of Bohart and Menke into two groups that he hypothesizes to be monophyletic. His one synapomorphy for the larger of these groups, which he calls Larridae, is a unique form of the openings of the larval salivary glands. This larval character was also stressed by Evans in his papers, and earlier by Michener (1952).

Many other authors have also been interested in phylogenetic relationships among sphecids wasps, and the preceding discussion is not intended to be an exhaustive historical review of ideas about sphecids relationships. However, the works mentioned above are especially noteworthy because of their comprehensive scope, their thoroughness, and the extent to which they have influenced other workers. Evans and co-workers have published several stimulating and frequently-cited papers discussing general evolutionary patterns among sphecids wasps (e.g. Evans 1957a, 1962, 1966a, 1966b,

1966c, Evans and West Eberhard 1970). In recent years, using phylogenetic patterns deduced from cladistic analyses to inform and evaluate theories about evolutionary processes has been more and more widely advocated as a fruitful research program (Eldredge and Cracraft 1980, Brooks and McLennan 1991, Harvey and Pagel 1991). The growing popularity of this approach makes it even more important to critically assess the strength of evidence supporting published phylogenetic hypotheses. The present paper is a quantitative cladistic analysis of the characters identified in the above-mentioned works of Evans (especially Evans 1959 and 1964a) and of Bohart and Menke (1976).

I did this study as background work for a research project with a narrower focus: a cladistic analysis of the genera in one subfamily, the Philanthinae. Thus, my major objective was to determine whether or not the Philanthinae as defined by Bohart and Menke is monophyletic and to establish its phylogenetic placement within the Apoidea (sensu Michener 1986 and Gauld and Bolton 1988 — i.e., sphecids wasps and bees). Unresolved relationships among taxa not closely related to the Philanthinae did not prevent me from continuing with my study, so I did not attempt to resolve them. A preliminary report of my analysis was published in a newsletter for aculeate researchers (Alexander 1990). I have received several inquiries about that report, and have also given more careful attention to problems involved with outgroup analysis, which have resulted in modified hypotheses of relationships within the Apoidea. The present paper is intended as a more complete presentation of what my exploratory analyses have revealed. Its major conclusion is that much more work remains to be done, but I hope it will also provide a better focus for that future work.

METHODS AND MATERIALS

As explained above, the starting point for this study was a series of tables of polarized characters taken from the works of Bohart and Menke (1976) and Evans (1959). The sphecids wasps belong to a monophyletic group (Apoidea) that also includes the bees (Apiformes). Characters to establish the monophyly of the Apoidea and Apiformes (bees) are based primarily upon Brothers (1975), supplemented by discussions in Bohart and Menke (1976) and Michener (1974).

I have not examined larval specimens myself, so

all my assignments of larval character states to taxa are based upon the literature. In addition to the numerous papers of Evans and co-workers cited earlier, Grandi's (1961) excellent illustrations of aculeate larvae are extremely useful. For bee larvae, I have relied primarily upon the descriptions by McGinley (1987). Evans' polarity assessments for larval characters are used, since information on larval morphology in the outgroup is unfortunately still too fragmentary for meaningful application of more rigorous analytical procedures.

For adult characters, I have examined specimens myself in order to determine the state of each character for each taxon, because such determinations cannot always be made from the literature. I have examined representatives of all the sphecids tribes recognized by Bohart and Menke (1976) and all genera for which both adults and larvae are known, as well as a few representatives of each of the major lineages of bees (traditionally assigned the rank of family). Appendix 1 lists the taxa whose adults I have examined.

In 1984, Day proposed that the puzzling genus *Heterogyna*, which was originally placed in its own monotypic family (Nagy 1969), is an aberrant sphecids wasp. It is not included in most of the analyses presented here, which deal with the taxa treated by Bohart, Menke, and Evans. However, I have recently been able to examine male specimens of four of the five known species of *Heterogyna*, and I accept Day's argument that the males of this genus exhibit the character states that Brothers identified as salient synapomorphies for sphecids wasps and bees, whereas the morphology of females is autapomorphic. I have done one preliminary analysis to determine the phylogenetic position of *Heterogyna* within Apoidea.

The final data matrix (Table 1) consists of ninety characters, of which ten are features of larval morphology, seventy-nine are features of adult morphology, and one is a feature of adult female behavior (character 72 in Table 2, which lists the characters and character states used in all the analyses).

I have selected outgroup taxa from lineages within the Aculeata, as discussed below. Exemplars from the Ichneumonidea represent an outgroup for the Aculeata, following the unpublished analyses of Mason (1983, cited by Carpenter [1986] and Gauld and Bolton [1988]) which hypothesize that the Aculeata and Ichneumonidea are sister taxa.

In each of the analyses presented below, a single

"hypothetical ancestor" is used as the outgroup for rooting the trees. Different hypothetical ancestors are used in different analyses. This is done to compare the results of analyses based entirely upon Bohart and Menke's judgments about the polarities of adult characters with the results of analyses based upon polarities that are hypothesized according to the procedure outlined by Maddison et al. (1984). The latter procedure determines the most parsimonious distribution of each character on a tree comprised of the ingroup and several outgroup taxa. For each character, this optimized character state distribution is used to hypothesize the state that was present in the ancestor of the ingroup. The tree that forms the basis for this procedure is assumed to be an independent and well-supported hypothesis of phylogenetic relationships among the outgroup taxa. In this type of analysis, the character being "fitted" to the tree is not used to derive the tree.

For my hypothesis, I have used the tree of aculeate relationships in Fig. 2 of Carpenter's (1990) reanalysis of the data in Brothers (1975). In my 1990 report in the newsletter *Sphecos*, I hypothesized the polarity of each character in my matrix as if the tree derived by Brothers and Carpenter were based upon characters completely independent of those I used in my analysis of relationships within the Apoidea. However, a closer examination of Brothers' data set shows that 23 of the 92 characters that he used in his study are also included in my matrix. Because his hypothesis of aculeate relationships is based on his assessment of the polarity of these characters, it would be logically inconsistent to use his phylogenetic hypothesis to postulate different polarities for these characters. Conflict about the state to be assigned to a given character at a given node — in this case, the node of interest is the common ancestor of the Apoidea — is possible because the most parsimonious distribution of a single character on a predetermined tree will not necessarily correspond to the optimized distribution of that character when it is used in conjunction with a large number of other characters in order to determine the most parsimonious tree for the entire set of characters. Consequently, for the characters in my matrix that Brothers also used in his study, the states that he hypothesized to be the groundplan state for the Apoidea (which he called the Sphecoidea in his paper) are assigned to the hypothetical ancestor in my matrix.

For most characters, the polarities hypothesized

Table 1. Data matrix used in the cladistic analyses. Characters and character states are defined in Table 2. "Outgroup 1" shows the codings used in the preliminary study published in Sphecos (Alexander, 1990), "Outgroup 2" is based on the polarities hypothesized by Bohart and Menke (1976), and "Outgroup 3" is based on the polarities determined by the character state optimization procedure of Maddison et al. (1984). For each taxon entry, the first number is character 0, the last is character 89. A "-" indicates that the character varies within the taxon (for the outgroup, these are characters for which polarity decisions are indecisive), and a "?" indicates that the state is unknown for the taxon (this is primarily used for larval characters, since larvae are undescribed for several taxa). (B and M = Bohart and Menke; optim. = optimized).

	0	1	2		3	4	5
Outgroup 1 (Sphecos)	0000000000-00000000000000-10-31			Aphilanthopini	000101001001010001000000100010		
Outgroup 2 (B and M)	0000000-0000100000000000000000--			Philanthini	0001010010010100000000102100000		
Outgroup 3 (optim.)	000000000000000000000000000010-31			Cercerini	0000-010011010110100000030101010		
Ampulicini	000001000210000000100000111120			Colletidae	010101000100-1000000010010-00-		
Dolichurini	0000000000100000000002000111021			Andrenidae	01-1010001000100000000001000--		
Sceliphriini	00000100010000000011-000000-11			Halictidae	01-10100010001000-0000001010--		
Sphecini	00011110010001-001100000000111			Melittidae	011101000100110000000000100000		
Ammophiliini	00011110010011-00-11-000000111			Long-tongued Bees	0111010001000100000-0-0010-0--		
Astatini	0000000000000000001110000000031			Laphyragogini	01010000110101000000000100030		
Pemphredonini	00-001-00-0-000001-1000010-0-1			Xenospecini	01110100110100000000000100110		
Psenini	0010000001020100011-000010100-			Dinetini	101101000100100000000000000011		
Mellinini	0000000000000000001110000000001			Helicocausini	0111010110010000100000100000		
Palarini	10010001100-000001110000100110			Entomosericini	101101001001011001200000010000		
Miscophini	0000000-00000000-110000-0000-			Eremiasphecini	0110100101010000000000000000-		
Larrini	1010000100000000011100000000000			Odontosphecini	0011010011010100000000100010		
Trypoxylini	01-0000-0-0-0-0111000000-0-			Pseudoscoliini	0101001001001100-00000100000		
Crabronini	00100-0-00-0-0001111-000-0-00			Scapheutini	101101001001010011000000101010		
Oxybelini	001010000000000001111011001230			Bothynostethini	01101001010-01100000000103000		
Alyssonini	0000000000000-0-00-110000111001			Heterogyna	01000000110000000000010010031		
Nyssonini	00000000010300000111100011230						
Gorytini	00-000000-00---011010000-1111						
Stizini	0010000001000110211101-0010111			Outgroup 1 (Sphecos)	6	7	8
Bembicini	10-120200-0000-021110120010111			Outgroup 2 (B and M)	010000-210100000-0100000000000		
Aphilanthopini	00000100010001110110000000-11			Outgroup 3 (optim.)	000-00200000000000000000000000		
Philanthini	010101000100011101100000000011			Ampulicini	010000200000000000000000000000		
Cercerini	00010100010101110110000010-10			Dolichurini	120000021010011112100000000002		
Colletidae	000100000100-11001111000000110			Sceliphriini	010000021010011112100000010002		
Andrenidae	0001100010001001111000010110			Sphecini	010010210010011112100000000000		
Halictidae	0-01110001000110011110000-0-10			Ammophiliini	010010210010011112100000000000		
Melittidae	000111000100011001111000010110			Astatini	00000002110100111021010101-0010		
Long-tongued Bees	000131-0010001100111100001-110			Pemphredonini	02-00012100100111-21--011--0110		
Laphyragogini	000010000040001100110000000011			Psenini	010000-2101001111210111010110		
Xenospecini	001100010-001-1002100000010012			Mellinini	010000021010011112101111030010		
Dinetini	001000010000000000110000000011			Palarini	01000121010011112101171010110		
Helicocausini	101000000000000001110000001232			Miscophini	00-0000-2101001111210111-020110		
Entomosericini	001100000100000001100000100121			Larrini	-100002--010011121011--020110		
Eremiasphecini	0001010000-000000-000000000011			Trypoxylini	01000002-010011112101111020110		
Odontosphecini	102101000000010011110000010011			Crabronini	021000021010011112101111020110		
Pseudoscoliini	00010100010000101110000010010			Oxybelini	02100102-010011112101111020110		
Scapheutini	0010010-000-000011110000-0-10			Alyssonini	010000021010011112101011111010		
Bothynostethini	00-010-0-00000011110000100010			Nyssonini	010100021010011112101000111012		
Heterogyna	0000000000000000001110000010002			Gorytini	--0-0-0-21010011112101001111011		
				Stizini	1101-0121010011112101000111010-		
				Bembicini	--01200210100111210100011101-		
Outgroup 1 (Sphecos)	0-0-0-02000-0000000-000101000000000			Aphilanthopini	0100000121010011112110111-1110		
Outgroup 2 (B and M)	0-0002000001000-000101000000000			Philanthini	010000121010011112110111111010		
Outgroup 3 (optim.)	01000200010000000-0-01000000000			Cercerini	010000-21010011112110111110110		
Ampulicini	200100010100100020201110100111			Colletidae	0-00000212111110210-0-010122		
Dolichurini	2101100000000000002201110000100			Andrenidae	0100002012111110210101-10122		
Sceliphriini	000010000010000110010110000110			Halictidae	0100002012111110210101-01-1-2		
Sphecini	00011000011-000110010110-0-10			Melittidae	01000012121111102101010-1001-2		
Ammophiliini	000100001111000110010110100110			Long-tongued Bees	010-001-11211111021-00--10-02		
Astatini	0011000010010000001000000000010			Laphyragogini	0000002200107111217???????		
Pemphredonini	00110-001000100--0-0-100001			Xenospecini	0100001210100111217???????		
Psenini	-01-01001-0-010010410000100000			Dinetini	2101001210100111217???????		
Mellinini	100100001-0010202100000100000			Helicocausini	0100001210100111217???????		
Palarini	00101001101010100-300001102010			Entomosericini	0101001210107111217???????		
Miscophini	10110-001-0-01000-0000001010--			Eremiasphecini	0100001210107111217???????		
Larrini	-0110-001-01-1000-00000101010			Odontosphecini	0100002210107111217???????		
Trypoxylini	10110-0010000100-0001001010--			Pseudoscoliini	0100001210100111217???????		
Crabronini	-01-0-00110-0100--000000101011			Scapheutini	110-001210107111217???????		
Oxybelini	10110110110101000100000101011			Bothynostethini	010-000210100111217???????		
Alyssonini	10010-001101012001000000101000			Heterogyna	2110000210100111217???????		
Nyssonini	101101011000000001-00000101000						
Gorytini	100101001--000001000000100000						
Stizini	1011010-11-1100001-00-00110010						
Bembicini	10-1010-11-1-100001001021-00-0						

Table 2. Characters and character states used in the parsimony analyses. Characters marked with an asterisk were treated as nonadditive (= unordered).

Character	Character States
0. Ocelli	0. Hemispherical, with transparent lens 1. Flattened, oval or linear, or reduced to a transverse scar
1. Inner margin of compound eyes	0. More or less parallel 1. Notched or emarginate
2.* Facets of compound eyes	0. More or less uniform in size 1. Some facets greatly enlarged ventrally or anteromedially 2. Facets enlarged dorsally, very small ventrally
3. Eyes (on maxilla)	0. Short and broad 1. Long and narrow
4. Galea-glossa complex	0. Short, broad, flap-like 1. Moderately elongated, not flap-like 2. Greatly elongated, subcylindrical 3. Greatly elongated, flattened, enclosed ventrally by labial palpi, which have the basal two segments greatly elongated and flattened, the apical two segments much shorter, subcylindrical
5. Mandibular socket	0. Open 1. Closed
6. Labrum	0. Short, wider than long, usually hidden by clypeus 1. About as long as wide 2. Longer than wide, extending well beyond clypeus
7. Externovenal tooth or notch on mandible	0. Absent 1. Present
8. Clypeus subdivided by distinct longitudinal lines	0. No 1. Yes
9*. Shape of clypeus	0. Narrowly transverse 1. Not transverse, but with a dorsally produced median portion 2. Sharply rooflike (Ampulicini) 3. Swollen, to accommodate proboscis when folded (Bembicini) 4. Not transverse, but with a ventrally produced median portion
10. Gular area	0. Narrow, so that hypostomal carina is close to occipital carina 1. Broad, hypostomal carina widely separated from occipital carina
11*. Frontal carina	0. Absent 1. Present, evenly convex in profile, linear in frontal view 2. Present, sharply angulate in profile, shaped like an inverted T in frontal view
3. Present, a very broad ridge rather than a narrow carina (Nyssonini)	
12. Frontal sulcus	0. Absent 1. Present
13. Antennal sockets	0. Contacting clypeus, or separated from it by less than half the diameter of a socket 1. Separated from clypeus by more than half the diameter of a socket
14. Subantennal sclerite delimited by subantennal sutures (= supraclypeal area of Michener, 1944)	0. absent 1. present
15. Clypeal brush (in males only)	0. absent 1. present
16*. Propleuron	0. Not specially modified 1. Posterolateral margin lamellate, posterolateral angle declivous and set off from rest of propleuron by inner ridge or hump 2. Anterior face flattened, somewhat compressed in lateral view, ventral margin and ventrolateral corner lamellate
17*. Pronotal collar	0. Long, not collar-like 1. Narrowly transverse, collar-like 2. Evenly sloping from neck of pronotum up to scutum, so that there is no discernible collar (Astatini)
18. Pronotal lobe	0. Contacting or nearly contacting tegula, so that scutum does not contact mesopleuron 1. Separated from tegula by anterolateral process or carina from scutum, so that scutum directly contacts mesopleuron
19. Notauli	0. Present, long 1. Absent or very short (not reaching an imaginary line tangent to anterior margins of tegulae)
20*. Admedian lines of scutum	0. Separate, distinct 1. Fused into a single median line 2. Absent
21. Oblique scutal carina	0. Absent 1. Present
22*. Scutellum	0. Without lateral flange 1. With lateral flange overlapping metanotum 2. A horizontal, strap-like band tightly appressed to metanotum, posterior margin lamellate
23. Metanotal squamae	0. Absent 1. Present
24. Scutellum with a pitted transverse basal sulcus	0. No 1. Yes
25. Episternal sulcus	0. Present, long (extending ventrad of scrobal sulcus) 1. Short (not extending ventrad of scrobal sulcus) or absent

26. *Omaulus*
 0. Absent
 1. Present
- 27*. Postspiracular carina
 0. A narrow, sharp ridge forming the vertical anterior wall of the subalar fossa
 1. A broad, rounded ridge forming the vertical anterior wall of the subalar fossa
 2. Absent, because subalar fossa is absent or separated into anterior and posterior pits
- 28*. Subalar line
 0. Absent or incomplete, but subalar area not reduced
 1. Present, but not greatly expanded into a carinate ridge or flange
 2. Present as a very prominent carina or flange
 3. Absent, subalar area greatly reduced or absent
- 29*. Separation of middle coxae
 0. Metasternum quadrate or rectangular, on more or less the same plane as mesosternum, so that midcoxae are widely separated
 1. Similar to 0, but metasternum distinctly narrowed anteriorly, so that midcoxae are close together
 2. Metasternum on a different plane from that of mesosternum
30. Posterior margin of metasternum
 0. Broadly rounded, truncate, or weakly emarginate
 1. Bilobed, lobes subparallel and closely approximated
 2. Bilobed, lobes diverging apically
31. Precoxal lobes
 0. Present, delineated by distinct transverse groove from mesosternal apophyseal pit
 1. Absent
32. Dorsolateral carina on middle coxa
 0. Absent
 1. Present
33. Lower metapleural area
 0. Present
 1. Absent
34. Propodeal sternite
 0. Absent
 1. Present
- 35*. Propodeal enclosure
 0. Present, U-shaped
 1. Present, V-shaped
 2. Absent
36. Propodeal mucro
 0. Absent
 1. Present
37. Lateral spines or teeth on propodeum
 0. Absent
 1. Present
38. Tarsal claws
 0. Bifid or with subapical teeth or lobe
 1. Simple
39. Plantulae
 0. Present
 1. Absent
40. Apicoventral setae on hindtarsomere V
 0. Setiform
 1. Bladelike
41. Foretarsal rake (in females)
 0. Absent
 1. Present
42. Tarsomeres
 0. IV similar to III, V inserted toward apex of IV
 1. IV short, V inserted dorsally at base of IV
43. Number of midtibial spurs
 0. Two
 1. One
- 44*. Apex of hind femur
 0. Unmodified
 1. Broadened, truncate
 2. With an apical spatulate process
45. Insertion of metasoma
 0. Between hind coxae
 1. After and above hind coxae
- 46*. Metasomal petiole
 0. Absent
 1. Formed of first metasomal sternum only
 2. Formed of first metasomal sternum and first metasomal tergum
- 47*. Base of first metasomal sternum
 0. Simple, without any carinae
 1. With longitudinal median ridge or paired ridges
 2. With distinct transverse ridge
- 48*. Shape of second metasomal sternum
 0. Evenly convex, not swollen at base
 1. Swollen at base, but without a transverse sulcus
 2. Swollen at base, with a transverse sulcus at base of swollen area
 3. Palarini — varies between sexes and species, but usually a very prominent subapical transverse ridge (especially in males)
 4. Similar to state 2, but with a pair of basilateral nodes bearing tufts of very short, fine setae
49. Lateral line or carina on tergum 1
 0. Present
 1. Absent
50. Number of visible metasomal terga in males
 0. Seven
 1. Fewer than seven
51. Pygidial plate (in females)
 0. Present
 1. Absent
- 52*. Sixth metasomal sternum (females)
 0. Similar to other segments, except for troughlike vertical side walls
 1. Elongate, forming an exposed tapering tube through which sting is exerted
 2. Apically bifid or emarginate
- 53*. Apex of female metasoma
 0. More or less conical
 1. Strongly compressed laterally
 2. Strongly compressed dorsoventrally
54. Cerci (males)
 0. Present
 1. Absent
55. Laterobasal spiracular lobes on male tergum 7
 0. Absent
 1. Present
- 56*. Volsella
 0. With differentiated digitus and cuspis
 1. Digitus and cuspis fused, not differentiated
 2. Absent
 3. A large, rolled, C-shaped plate (*Bothynostethini*)
57. Penis valves (= "aedeagal head")

0. Without teeth on apicoventral edge
1. With numerous short teeth on apicoventral edge
- 58*. Apex of marginal cell
 0. Acuminate, ending on costal margin of wing
 1. Evenly truncate or broadly rounded
 2. Open (in some outgroup taxa)
 3. Obliquely truncate, not ending on costal margin of wing
59. Number of submarginal cells
 0. Three
 1. Two or fewer
- 60*. Forewing vein 3rs-m ("outer veinlet of 3rd submarginal cell" in Bohart & Menke, 1976)
 0. Ending near middle of marginal cell (= R1 cell)
 1. Ending near apex of marginal cell
 2. Absent
- 61*. Forewing vein 2-Rs ("outer veinlet of 1st submarginal cell" in Bohart & Menke, 1976)
 0. Angled, and with a remnant of vein 1r-rs (1st radial cross-vein)
 1. Straight or weakly curved, not appendiculate, no remnant of 1r-rs
 2. Absent
62. Number of discoidal cells in forewing
 0. Three
 1. Two or fewer
63. Divergence of forewing vein M
 0. At or after vein cu-a
 1. Before vein cu-a
64. Prestigmal length of 1st submarginal cell
 0. Less than twice height of cell
 1. Between two and three times height of cell
 2. More than three times height of cell
65. Submarginal and discoidal cells
 0. Separated by vein Rs+M
 1. Fused, due to loss of vein Rs+M
66. Jugal lobe
 0. Small or absent
 1. About 1/2 as long as vannal lobe
 2. More than 3/4 as long as vannal lobe
67. Hind wing vein 2A
 0. Present as a tubular vein
 1. Present as a nebulous or spectral vein
 2. Absent
68. Hind wing vein 3A
 0. Present
 1. Absent
69. Body vestiture
 0. Without plumose setae
 1. With at least some plumose setae
70. Female metasomal tergum 7
 0. Somewhat exposed, evenly sclerotized throughout
 1. Retracted and entirely hidden from external view, sclerotization reduced to a short strip across anterior margin
 2. Sclerotization entirely reduced mesally so that the lateral spiracular plates (hemitergites) are linked by membrane only
71. Female hind basitarsus
 0. Subcylindrical, about as wide as tarsomeres II - V
 1. Flattened, wider than tarsomeres II - V
72. Larval provisions
 0. Arthropods (usually paralyzed)
 1. Pollen and nectar or plant oils
73. Posterolateral angle of pronotum
 0. Evenly rounded or subacute, reaching tegula
 1. Reduced dorsally above and slightly anterior to spiracular operculum; operculum forms a highly differentiated pronotal lobe
74. Ventral angle of pronotum
 0. Rounded, not much exceeding level of base of fore coxa
 1. Greatly produced, almost contacting its counterpart ventrally
75. Metapostnotum
 0. Forming a transverse groove at anterior margin of propodeum
 1. Greatly enlarged and posteriorly produced mesally, forming a "propodeal enclosure" or "propodeal triangle"
76. Hindtibial strigilus
 0. Absent
 1. Present
- 77*. Hind margin of pronotum
 0. Pronotum long, hind margin nearly straight, only very slightly anteriorly arcuate
 1. Pronotum shortened, hind margin strongly concave in a fairly regular and somewhat arcuate parabolic curve ("V-shaped")
 2. Pronotum shortened, hind margin shifted anteriorly over almost its entire width ("broadly U-shaped")
78. Prosternum
 0. Forming an approximately uniform plane, not sunken
 1. Sunken over most of its surface, only a short anterior section visible ventrally
79. Larval integument
 0. Smooth
 1. With abundant setae or dense spinules
80. Larval body shape
 0. With more or less even contours
 1. With conspicuous projections laterally, dorsally, or caudally
81. Position of larval anus
 0. Terminal, directed caudad
 1. Ventral, preapical, directed ventrad
82. Opening between atrium and sub-atrium of larval spiracles
 0. Armed with a circlet of spines
 1. Simple, unarmed
83. Parietal bands (on head of larva)
 0. Present
 1. Absent, or very faintly indicated
84. Larval antennal papillae
 0. Absent
 1. Present
- 85*. Larval mandibles
 0. Simple, with 4 or 5 apical teeth
 1. With fewer than 4 or 5 teeth
 2. With an apical concavity
 3. As in Mellinini (autapomorphy)
86. Larval maxillae
 0. Directed mesad apically, closely associated with labium and hypopharynx
 1. Projecting apically as large, free lobes
87. Larval galea

- 0. Large
- 2. Small
- 88*. Larval spinneret
 - 0. A transverse slit
 - 1. With paired openings, each at the end of a projection
 - 2. Absent
- 89. Male metasomal sternum 7
 - 0. Well developed, not much smaller than sternum 6, usually clearly visible externally and exposed
 - 1. Reduced and much smaller than sternum 6, but partly exposed
 - 2. Greatly reduced, much smaller than sternum 6 and completely hidden by it
 - 3. Absent

by Bohart and Menke are supported by the more rigorous analytical procedure described above. Table 3 lists the seven characters for which the optimization procedure results in a different polarity assessment from that hypothesized by Bohart and Menke. There are an additional twelve characters for which one procedure yields uncertain or equivocal results, whereas the other hypothesizes a single unequivocal groundplan state. Thus, a total of nineteen characters do not receive identical polarity codings with each procedure.

A few of the optimized polarity decisions are at odds with rather widely accepted ideas about character evolution in sphecids wasps and bees. Especially noteworthy in this respect are the episternal sulcus (character 25), plantulae (character 39), and foretarsal rake (character 41).

Bohart and Menke hypothesize that an episternal sulcus extending ventrad of the scrobal sulcus is the plesiomorphic condition for the Sphecidae, and bee systematists have generally regarded this character state as plesiomorphic for bees. For both groups, the basis of this assessment seems to be that a long episternal sulcus is present in taxa which generally have plesiomorphic states for other characters. Most taxa outside the Apoidea have no sulcus at all in the position of the episternal sulcus, but some Bethyridae (e.g. *Epyris clarimontis*) may have one. My analyses use Bohart and Menke's coding of "episternal sulcus absent or short" (Character 10 in their Table 2, p. 30; Character 25, state 1 in my Table 2) as a single character state. Under this coding, outgroup taxa are scored as having the episternal sulcus absent (or variable in Bethyridae), and the character state optimization procedure infers that the ancestor of the Apoidea had the episternal sulcus "absent or short". If

Table 3. Characters for which Bohart and Menke (1976) postulated different groundplan states from those derived by an optimized fit to a cladogram of aculeate taxa based on the studies of Brothers (1975) and Carpenter (1990), using the optimization procedure presented by Maddison et al. (1984). Characters and character states are defined in Table 2, and are merely given brief labels here. The column labelled "B & M" shows the groundplan state postulated by Bohart and Menke. This column corresponds to Outgroup 2 in Table 1. A "?" indicates that Bohart and Menke expressed doubt as to the plesiomorphic condition for the character, or did not indicate what they considered the plesiomorphic state to be. The column labelled "Optimized" shows the state assigned to the ingroup node (i.e. the state present in the ancestor of the Apoidea) as determined by the optimization procedure mentioned above. This column corresponds to Outgroup 3 in Table 1. Characters in this column denoted by a (B) are ones that Brothers used in his study, so that groundplan states for these characters are based upon his polarity assessments rather than the tree-fitting procedure of Maddison et al. (1984). Characters denoted by a "-" in this column and the "Sphecoc" column are those for which polarity decisions were indecisive. The column labelled "Sphecoc", equivalent to Outgroup 1 in Table 2, shows the groundplan states used in a preliminary analysis that I published in the newsletter Sphecoc (Alexander, 1990). In that analysis, I did not distinguish between characters in my data matrix that had and had not been used by Brothers in his study. Instead, the groundplan state of each character was determined by optimizing its fit to Brothers' cladogram, regardless of whether or not the character had been used to derive the cladogram.

Character	Sphecoc	B&M	Optimized
7. Mandibular notch	0	?	0
10. Gular area	-	0	0
12. Frontal sulcus	0	1	0
24. Scutellar sulcus	-	0	0
25. Episternal sulcus	1	0	1
29. Separation of midcoxae	0	?	1 (B)
31. Precoxal lobes	-	?	1
33. Lower metapleural area	-	0	0 (B)
39. Plantulae	-	0	1
41. Foretarsal rake	0	1	0
45. Insertion of metasoma	0	?	0
47. Base of sternum 1	-	0	-
49. Lateral line on tergum 1	-	1	-
61. Forewing vein 2-Rs	1	0	1
63. Divergence of vein M	0	?	0
66. Jugal lobe	-	2	2 (B)
67. Hind wing vein 2A	2	0	0 (B)
68. Hind wing vein 3A	1	0	0 (B)
76. Hindtibial strigilus	-	0	0

“absent” and “short” were coded as separate character states, the groundplan state for Apoidea would be equivocal, because the ingroup would have two derived states, neither of which occurs in the outgroup.

A similar argument explains the hypothesis that the absence of a foretarsal rake in females is plesiomorphic. In the outgroup taxa that I have examined, only Anthoboscinae and some Pompilidae have a foretarsal rake. In Brothers’ original (1975) analysis, Apoidea and Vespoidea are sister taxa, and the first clade to branch off within Vespoidea is (Tiphidae [with Anthoboscinae as the basal group] + (Sapygidae + Mutillidae)). In Carpenter’s (1990) reanalysis of Brothers’ data, Sierolomorphidae is the basal clade in Vespoidea. Females of Anthoboscinae, and some Sapygidae I have examined for this character (e.g. *Fedtschenkia anthracina*), have a foretarsal rake. Thus, if Brothers’ original hypothesis of aculeate relationships is correct, the ancestral state of the foretarsal rake in Apoidea would be equivocal. Carpenter’s cladogram supports the conclusion that the ancestor of Apoidea had no foretarsal rake.

In the outgroup, I find plantulae to be present in Pompilidae, Anthoboscinae, and some Rhopalosomatidae. Such a distribution results in the hypothesis that plantulae are primitively absent in Apoidea if Carpenter’s cladogram is used. If

Brothers’ cladogram is used, the groundplan state for Apoidea is equivocal.

With the basic data matrix of Table 1, I have performed analyses to examine the effects of altering three variables: the taxa examined, the characters employed, and the groundplan character states for the hypothetical ancestor. The two different groups of taxa considered are (1) only those for which both adults and larvae have been described, and (2) all sphecids tribes, including those for which only adults are known. Including taxa for which only adults are known in an analysis that uses larval characters results in a data matrix with numerous “empty” cells (denoted by a “?” in Table 1). Although I use a parsimony program (Hennig86) that can analyze a matrix with missing information, the usual result of doing such an analysis is poorer resolution of phylogenetic relationships. The alternative is to completely ignore certain taxa because of insufficient information about them. Neither approach is completely satisfactory. By comparing the results of both approaches, one can at least find out if there are any patterns of phylogenetic relationships supported by both sets of incomplete information.

A similar rationale explains why I wish to compare the results of analyses that use both adult and larval characters with the results of analyses that use only adult characters. Finally, I examine the results of using a hypothetical ancestor based upon

Table 4. Combinations of variables employed in the quantitative cladistic analyses. For hypothetical ancestor codings, the column labelled “Literature” utilized codings hypothesized in the literature, primarily by Bohart and Menke (1976) and Evans (1959), and the column labelled “Optimized” utilized codings based upon the procedures described by Maddison et al. (1984), as explained in the text. For each of the analyses designated by number in the table, there was also a part (a) in which all characters were given equal weight, and a part (b) in which successive approximations character weighting was used. Thus, Analysis 1b used hypothetical ancestor codings based on the literature, only sphecids tribes whose larvae are known, adult and larval characters, and successive approximations character weighting.

TAXA EMPLOYED	HYPOTHETICAL ANCESTOR CODINGS	
	LITERATURE	OPTIMIZED
Only sphecids whose larvae are known	Analysis 1: Adult & larval characters	Analysis 5: Adult & larval characters
	Analysis 2: Adult characters only	Analysis 6: Adult characters only
All Sphecids Tribes	Analysis 3: Adult & larval characters	Analysis 7: Adult & larval characters
	Analysis 4: Adult characters only	Analysis 8: Adult characters only

the polarity decisions of Bohart and Menke with the results of using a hypothetical ancestor based upon polarity decisions derived from character state optimization. This $2 \times 2 \times 2$ arrangement of variables requires eight basic analyses. For each of these analyses, I also compare the results obtained when all characters are given equal weight with the results obtained when characters are weighted according to Farris' (1969) successive approximations procedure. Table 4 summarizes the combinations of variables used in each analysis.

As explained above, the assessments of character polarities made by Bohart and Menke agree with the results of a more formal analytical procedure for all but 19 of the characters included in the data matrix that I used. I therefore also examine the results of an analysis that excludes these 19 characters (the characters are listed in Table 3). For this analysis, I include all sphecid tribes and both adult and larval characters (except for the 19 characters just mentioned). The analysis including *Heterogyna* uses all sphecid tribes, adult and larval characters (the latter coded as unknown for *Heterogyna* and 10 other tribes), and the character state optimization procedure for outgroup analysis.

All analyses discussed below employed J.S. Farris' Hennig86 program, Version 1.5 (Farris 1988), and used the commands m^* and bb^* to search for the most parsimonious trees. Use of the bb^* option was time-consuming, especially when numerous iterations were necessary in the successive approximations character weighting procedure. (According to Farris [1988], the bb command will not retain more than 100 minimum-length trees that are found in an extended branch-swapping procedure, whereas the bb^* command will retain all minimum-length trees.) Comparison of results obtained with the bb and bb^* commands for the same data set showed that they resulted in different final weights assigned to some characters and thus different hypotheses of phylogenetic relationships. In view of this, I considered it preferable to use the more exhaustive branch-swapping procedure, under the assumption that it was taking complete account of all the available information, instead of using an arbitrary cut-off point in searching for multiple minimum-length trees.

In these analyses, the tribes of Sphecidae as defined by Bohart and Menke are used as the terminal taxa. This taxonomic level has been selected primarily for reasons of analytical tractabil-

ity. Bohart and Menke recognize 226 genera and 7,634 species of sphecid wasps, so even an analysis at the level of the genus would require an extremely large and cumbersome matrix. Grimaldi (1990) reported an attempt to analyze a matrix with 158 taxa in the dipteran family Drosophilidae using the Hennig86 program. He found that "initial runs ... using the complete matrix were never finished, so the matrix was gradually pared down until it was found that 127 taxa was the maximum number that the program could analyze (at least using the m^* ; bb commands)." The analytical tractability of a data matrix depends not only on the number of taxa, but also on the level of character conflict, with high levels of character conflict resulting in poor resolution, or multiple equally parsimonious resolutions. The results to be presented below show high levels of character conflict.

The major shortcoming of using tribes (or genera) as terminal taxa is that several of them are almost certainly paraphyletic, and treating such taxa as monophyletic adds yet another source of error and confusion in a phylogenetic analysis. Table 5 lists the tribes of sphecid wasps that are most likely to be paraphyletic, because they are defined by character states that Bohart and Menke themselves regard as plesiomorphic at the level of the tribe they define. Because of uncertainty about which tribes are monophyletic, a few of the characters in the matrix I used are autapomorphies. Although such characters are not useful for determining phylogenetic relationships among tribes, they do provide evidence that the tribe possessing them is monophyletic. Even with autapomorphies, the consistency indices for these analyses are low enough that anyone who erroneously tries to use this index as a measure of confidence in a phylogenetic hypothesis should be unlikely to develop a false confidence in these particular hypotheses.

RESULTS

Each of the analyses results in numerous equally parsimonious trees (range: 9 to 5,272 trees; tree statistics summarized in Table 6). Thus, the first conclusion is that these data provide support for a large number of competing hypotheses about phylogenetic relationships within the Apoidea. Figures 1-10 summarize the results of each analysis in a manner that facilitates comparison, although it is important to remember that the diagrams being compared are consensus trees, and that the actual

Table 5. Tribes in Bohart and Menke's (1976) classification that are defined by characters that they considered to be plesiomorphic at the level of the tribe.

TRIBE	COMMENTS
Sceliphirini	Apparently paraphyletic with respect to Sphecini + Ammophilini. Bohart and Menke interpreted the presence of plantulae in the Sphecinae as plesiomorphic, but the optimization procedure for establishing character polarity would interpret the presence of plantulae as an autapomorphy for Sceliphirini, although this character exhibits high levels of homoplasy.
Astatini	Includes all genera of subfamily Astatinae except <i>Dinetus</i> .
Miscophini	Apparently paraphyletic with respect to other tribes of Larrinae.
Crabronini	Apparently paraphyletic with respect to Oxybelini.
Gorytini	Apparently paraphyletic with respect to other tribes of Nyssoninae.
Stizini	Apparently paraphyletic with respect to Bembicini.
Aphilanthopini	Apparently paraphyletic with respect to other tribes of Philanthinae.

number of competing hypotheses is far higher than what is shown pictorially. Appendix 2 presents a brief discussion of the ambiguities involved in mapping character state distributions onto consensus trees.

Despite the large number of competing hypotheses that merit consideration, a few consistent patterns appear in all the analyses. Table 7 identifies groupings of terminal taxa that are consistently supported as monophyletic groups, and lists the characters that are always interpreted as synapomorphies for these groups. It seems reasonable to regard these groups as strongly supported by the available evidence, and it is noteworthy that most of them are groups that have long been regarded as "natural" and are similar or identical in composition to the subfamilies in Bohart and Menke's classification. Table 8 compares the monophyletic groups consistently supported in this study with the classification proposed by Bohart and Menke.

Just as noteworthy as the groupings of sphecid tribes that are consistently supported as monophyletic are traditional groupings that receive little or no support as monophyletic taxa. Judging from

Table 6. Summary statistics for the analyses defined in Table 4; C.I. = consistency index, R.I. = retention index. Analysis 9 used all sphecid tribes and both adult and larval characters, but excluded the nineteen characters listed in Table 3. "Heterogyna" refers to the analysis including the enigmatic genus *Heterogyna*.

		Length	C.I.	R.I.	No. of Trees
Analysis	1a	274	.44	.65	5272
	1b	726	.73	.84	108
Analysis	2a	242	.44	.63	42
	2b	633	.75	.83	99
Analysis	3a	346	.37	.60	3994
	3b	686	.72	.85	3994
Analysis	4a	314	.37	.58	3994
	4b	609	.70	.82	347
Analysis	5a	273	.44	.65	555
	5b	722	.73	.83	162
Analysis	6a	244	.44	.62	854
	6b	654	.77	.84	90
Analysis	7a	347	.37	.60	156
	7b	669	.72	.84	330
Analysis	8a	316	.37	.58	15
	8b	597	.70	.82	46
Analysis	9a	248	.41	.64	2009
	9b	570	.74	.86	3992
Heterogyna	a	356	.36	.60	351
	b	698	.68	.82	9

the results of these analyses, the subfamilies Pemphredoninae and Astatinae of Bohart and Menke's classification do not appear to be monophyletic. Each of these subfamilies consists of two tribes (one of the tribes of Astatinae is monotypic). Character states that Bohart and Menke use to unite these tribes into subfamilies appear to be plesiomorphic. The monophyly of each tribe was not investigated in this study.

One final general observation is that very few consistent and strongly supported patterns of relationships among major monophyletic groups within the Apoidea are found. In Figures 1-10, many of the internal branches are supported by very few characters, and most of these characters exhibit homoplasy.

The group of three tribes corresponding to Bohart and Menke's subfamily Sphecinae is consistently a basal lineage, and most of the remaining tribes share a substantial number of synapomorphies. The Ampulicinae of Bohart and Menke is a problematic group in this respect, however. In most of the analyses in which only adult characters are used, the Ampulicinae is placed in monophyletic groupings that also include several

Table 7. Groupings of terminal taxa that were consistently supported as monophyletic groups, and characters that were consistently hypothesized to be synapomorphies for each group. Character states are numbered as in Table 2.

AMPULICINAE (Ampulicini + Dolichurini)

- 24-1 Pitted transverse basal sulcus on scutellum (also occurs in nine other tribes, may vary within tribes).
- 28-2 Subalar line a very prominent carina or flange (also in Entomosericini).
- 30-2 Posterior margin of metasternum distinctly bilobed, lobes diverging apically.
- 48-2 Metasomal sternum 2 swollen at base, with a transverse sulcus or carina (also in Entomosericini).
- 50-1 Male with fewer than seven visible metasomal segments.

SPHECINAE (Sceliphri + (Sphecini + Ammophilini))

- 5-1 Mandibular socket closed (also in Ampulicini, Pemphredonini, Scaphetini, most Philanthinae and bees, some Crabronini).
- 34-2 Propodeal sternite present (also in Dolichurini).
- 40-1 Apicoventral setae on hindtarsomere V blade-like (varies within Gorytini, Stizini, and Bembicini).
- 45-1 Insertion of metasoma after and above hind coxae (also in Dolichurini, according to Bohart and Menke).
- 46-1 Metasomal petiole formed of sternum 1 only (also in Psenini, and in some Pemphredonini, Trypoxylini, and Crabronini).
- 64-1 Prestigial length of first submarginal cell less than twice height of cell (also in some Gorytini and Stizini).

Sphecini + Ammophilini

- 3-1 Stipes long and narrow (also in Palarini, Bembicini, Entomosericini, Xenospecini, bees, most Philanthinae).
- 4-1 Galea-glossa complex long and narrow (also in Oxybelini, bees except Colletidae).
- 6-1 Labrum subquadrate.
- 13-1 Antennal sockets separated from clypeus by more than half the diameter of the socket (also in Psenini, Stizini, Laphyragogini, Odontospecini, Xenospecini, bees, most Philanthinae, some Trypoxylini and Gorytini).

APIFORMES (Bees)

- 20-1 Admedian lines of scutum fused into a single median line.
- 27-1 Postspiracular carina a broad, rounded ridge forming the vertical anterior wall of subalar fossa (interpreted as a reversal in these analyses).
- 38-0 Tarsal claw bifid or with subapical teeth or lobes (interpreted as a reversal in these analyses).
- 41-0 Foretarsal rake absent (interpreted as a reversal in these analyses).
- 69-1 Body vestiture including some plumose hairs.
- 70-2 Female metasomal tergum 7 divided into hemitergites.
- 71-1 Female hind tarsus flattened, wider than more distal tarsomeres.
- 72-1 Larval provisions consist of pollen and nectar or plant oils.

- 89-2 Male metasomal sternum 7 greatly reduced, much smaller than sternum 6 and completely hidden by it.
- 88 Larval spinnerets: variable, but never with paired openings, each at the end of a projection, so this character is interpreted as undergoing reversal in these analyses. (By comparison, Lomholdt (1982) interpreted the absence of paired spinnerets in bees as plesiomorphic.)

PHILANTHINAE s. str. (Aphilanthopini, Philanthini, Cercerini, Pseudoscoliini)

- 15-1 Male with a clypeal brush.
- 32-0 Middle coxae without a dorsolateral carina or crest (interpreted as a reversal in these analyses).
- 86-1 Larval maxillae projecting apically as free lobes (also in Nyssoninae).

APIFORMES + PHILANTHINAE

- 14-1 Delimited subantennal sclerite

NYSSONINAE s.str. (Nyssonini, Gorytini, Stizini, Bembicini)

- 21-1 Oblique scutal carina (in all analyses except 8b, in which these tribes are a paraphyletic assemblage).
- 82-0 Opening between atrium and subatrium of larval spiracles armed with a circlet of spines (interpreted as a reversal in these analyses).

Stizini + Bembicini

- 16-2 Propleuron with anterior face flattened, somewhat compressed in lateral view, ventral margin and ventrolateral corner lamellate

AMPULICINAE + SPHECINAE

(sister taxa only in Analyses 3b, 5b, 6b, and 7b)

- 9-1 Clypeus not transverse, but with dorsally produced median portion (further modified in Ampulicini)
- 52-1 Female metasomal sternum 6 elongate, forming an exposed tapering tube through which sting is exerted.
- 57-1 Penis valves with small teeth on ventral edge.
- 76-1 Hindtibial strigulus present (also present in most other Apoidea except Apiformes).

tribes traditionally assigned to the Nyssoninae.

Such a relationship has been suggested before, on the basis that the scutum overlies the tegula (Pate 1938), although Pate himself expressed reservations about this relationship. Most sphecoid workers have not accepted the hypothesis of a close relationship between the Ampulicinae and Nyssoninae. It is worth noting that in the analyses hypothesizing that the Ampulicinae are part of the Nyssoninae (usually the sister group of Nyssonini), none of the putative synapomorphies for these taxa are unique to them. The characters consistently hypothesized as synapomorphies are presence of an omalus (character 26-1 in Table 2); loss of a foretarsal rake (41-0, shared by Ampulicinae

Table 8. A comparison of Bohart and Menke's (1976) subfamilial classification of sphecids wasps with tribal groupings that were consistently hypothesized as monophyletic in this study. Monotypic subfamilies in Bohart and Menke's classification are not listed here, because in this study they were assumed to be monophyletic by definition.

BOHART AND MENKE	THIS STUDY
AMPULICINAE (tribes Ampulicini and Dolichurini)	Same as in Bohart & Menke
SPHECINAE (tribes Sceliphriini, Sphecini, and Ammophilini)	Same as in Bohart & Menke
PEMPHREDONINAE (tribes Psenini and Pemphredonini)	Monophyletic group only in consensus trees from Analyses 7a and 8a.
ASTATINAE (tribes Astatini and Dinetini)	Not a monophyletic group in any consensus trees.
LARRINAE (tribes Larrini, Palarini, Miscophini, Trypoxylini, Bothynostethini, and Scapheutini)	A monophyletic group of only these tribes was not consistently supported in all analyses, but many tribes of Bohart & Menke's Larrinae and Crabroninae frequently formed a monophyletic assemblage. The assemblage sometimes also included Alyssonini, Melliniini, and/or Heliocausini, and Larrini and Palarini were sometimes <i>not</i> included with the other tribes.
CRABRONINAE* (tribes Crabronini and Oxybelini)	*Menke (1988) now advocates including Oxybelini and Crabronini with the Larrinae, and no longer recognizes the subfamily Crabroninae.
NYSSONINAE (tribes Melliniini, Heliocausini, Nyssonini, Alyssonini, Gorytini, Bembicini, Stizini)	The tribes Nyssonini, Gorytini, Stizini, and Bembicini consistently formed a monophyletic assemblage, although this assemblage sometimes also included Ampulicini, Dolichurini, Entomosericini, and/ or Psenini.
PHILANTHINAE (tribes Eremiasphecini, Philanthini, Aphilanthopini, Odontosphecini, Pseudoscoliini, CERCERINI)	Aphilanthopini, Philanthini, Pseudoscoliini, and Cercerini consistently formed an exclusive monophyletic assemblage. Eremiasphecini and Odontosphecini were never included in this assemblage.

and Nyssonini, the latter group consisting of cleptoparasites); hind wing jugal lobe small or absent (66-0); and male metasomal sternum 7 greatly reduced and hidden by sternum 6 (89-2). In analyses that hypothesize a sister group relationship between Ampulicinae and certain Nyssoninae, the ancestor of Ampulicinae is required to undergo numerous character state reversals, including loss of the oblique scutal carina (21-1). This character is unique to the tribes Bembicini, Gorytini, Nyssonini, and Stizini, which means that in this study it is a major character supporting the monophyly of these four tribes as a group ("Nyssoninae" in a narrow sense). The carina is not present in all members of Gorytini. Because this tribe is paraphyletic, the phylogenetic significance of the absence of the carina in some gorytine genera is unclear.

Many of the analyses in which both adult and larval characters are used hypothesize a sister group relationship between the Ampulicinae and the Sphecinae. Although Evans (1959, 1964) emphasizes the similarities in the larvae of these two groups, these similarities are features that he considers plesiomorphic, and in my analyses all the characters suggesting a sister group relationship between the two groups are features of adult morphology. The most frequently hypothesized synapomorphies are the dorsally produced clypeus (9-1), female metasomal sternum 6 forming a tube through which the sting is exerted (52-1), toothed penis valves (57-1), and presence of a hindtibial strigilus (76-1, also present in most other sphecids, but independently derived in Ampulicinae + Sphecinae if they are sister taxa).

Apart from the basal position of the Sphecinae

(and probably the Ampulicinae), the other consistent result of these analyses is a close relationship between the bees and the Philanthinae (i.e. tribes Aphilanthopini, Cerцерini, Philanthini, and Pseudosoliini — the tribes Eremiasphēcini and Odontosphēcini, which Bohart and Menke placed in the Philanthinae, do not form a monophyletic grouping with these other four tribes in my analyses). In analyses that include all sphecids tribes, one or more of the following tribes are occasionally included in a monophyletic group that also contains the bees and Philanthinae: Psenini, Pemphredonini, Laphyragagini, and Xenosphēcini (the last two tribes each contain one genus). Only one character is consistently hypothesized as a synapomorphy of bees and philanthines in all the analyses. This is a feature referred to by Bohart and Menke as a "delimited subantennal sclerite", which is equivalent to what bee specialists (following the terminology of Michener 1944) call the "supraclypeal area", and is not the same as Michener's "subantennal area". Perhaps it would be less confusing to think of this character in terms of the presence or absence of a subantennal suture extending from the dorso-lateral angle of the clypeus toward the antennal socket. Other characters hypothesized as synapomorphies of bees and philanthines in some, but not all, of the analyses are: elongated stipes (character 3-1), a closed mandibular socket (5-1), antennal sockets not contacting the clypeal margin (13-1), subalar line present but not specially modified (28-1, interpreted as a reversal when hypothesized as a synapomorphy), and larval mandibles with a reduced number of apical teeth (85-1).

One other way to summarize the results of these analyses is to consider the performance of individual characters. Apart from autapomorphies (either at the level of terminal taxa or of the Apoidea as a taxon), which can never support conflicting phylogenetic hypotheses, there are some characters that consistently support the same hypotheses in all analyses, and others that perform quite erratically. The successive approximations character weighting procedure takes this into account by assigning weights to characters according to their level of homoplasy in a parsimony analysis. Consequently, one way to summarize a complex body of information about character performance in a series of parsimony analyses is to compare the final weights assigned to each character in each analysis. Table 8 provides such a summary for the characters used in this study.

DISCUSSION

In the title of this paper, I have described this study as "exploratory". It is based upon definitions of characters and character states that are not well suited for cladistic analyses because they confound two different ways of thinking about character evolution, viz. homology and degree of divergence from an ancestral condition. Both types of character change are clearly part of evolution, but in order to properly describe either one, it is important to distinguish between them. In their tables, Evans, Bohart, and Menke treat all derived character states as equivalent, even in cases where it is very unlikely that they consider them homologous. For example, Bohart and Menke's definition of character states for the mouthparts (their Table 2, p. 30) is "mouthparts short" (plesiomorphic) and "mouthparts elongate or unusually modified" (apomorphic). If this is coded as a simple two-state character, as in Bohart and Menke's table, and used in a quantitative parsimony analysis, one is hypothesizing that the elongate mouthparts of Bembicini, in which the galea and glossa are lengthened but the stipes and prementum are relatively unmodified, are homologous to the elongate mouthparts of Philanthinae, in which the galea and glossa are short but the stipes and prementum are lengthened. Bohart and Menke did not intend their table to be interpreted in this way (A.S. Menke, personal communication), and my analysis makes some preliminary attempts to redefine their characters in a way that comes closer to identifying similarities that are likely to be homologous. However, there is a great need in sphecids systematics for careful comparative morphological studies such as the work on bee mouthparts that has been published in recent years, which has had the explicit goal of identifying homologous character states (Winston 1979, McGinley 1980, Michener and Brooks 1984; also see Bohart and Menke 1976 p. vii).

Neither a cladist nor an evolutionary taxonomist ever knows with absolute certainty whether or not a given shared similarity is really a synapomorphy. This is why parsimony analyses are done (Farris 1983). However, it does seem likely that a character analysis explicitly intended to distinguish between homologous and homoplastic similarities might do so more effectively than a character analysis that considers both types of similarity equally informative. A parsimony analysis utilizing the data that are supposed to form the basis of our existing

Table 9. Descriptive statistics for the weights assigned to each character by the successive approximations procedure in Analyses 1-9. Characters marked with an asterisk were not used in Analysis 9.

Character	Weight		
	Mean	Median	Range
0. Ocelli	0.89	0	0-2
1. Inner margins of eyes	0	0	always 0
2. Eye facets	0.89	1	0-2
3. Elongated stipes	0.56	1	0-1
4. Galea-glossa complex	1	1	always 1
5. Mandibular socket	0.44	0	0-1
6. Labrum	3	3	always 3
*7. Mandibular notch	5	5	0-10
8. Tripartite clypeus	10	10	always 10
9. Shape of clypeus	3.67	3	3-5
*10. Gular area	10	10	always 10
11. Frontal carina	10	10	always 10
*12. Frontal sulcus	2.50	0	0-10
13. Antennal sockets	1.33	1	1-2
14. Subantennal sclerite	2.78	2	1-4
15. Male clypeal brush	9.11	10	2-10
16. Propleuron	4.56	3	2-10
17. Pronotal collar	2.67	3	1-4
18. Pronotal lobe	0	0	always 0
19. Notauli	0.89	0	0-2
20. Admedian lines	3	3	always 3
21. Oblique scutal carina	6.44	10	1-10
22. Scutellum	10	10	always 10
23. Metanotal squamae	10	10	always 10
*24. Scutellar sulcus	0	0	always 0
*25. Episternal sulcus	0.13	0	0-1
0. Omaulus	0.44	0	0-2
27. Postspiracular carina	1	1	always 1
28. Subalar line	1.33	1	0-3
*29. Separation of midcoxae	0.88	1	0-1
30. Metasternum	5.89	1	0-1
*31. Precoxal lobes	2.63	2	1-4
32. Midcoxal carina	0.33	0	0-1
*33. Lower metapleural area	0.75	0	0-2
34. Propodeal sternite	3	3	always 3
35. Propodeal enclosure	4.67	5	3-10
36. Propodeal mucro	10	10	always 10
37. Propodeal spines	0.44	0	0-2
38. Tarsal claw	1.67	2	1-2
*39. Plantulae	0	0	always 0
40. Setae on hindtarsomere V	10	10	always 10
*41. Female foretarsal rake	0	0	always 0
42. Tarsomeres	0	0	always 0
43. Midtibial spurs	1	1	0-2
44. Apex of hind femur	4	2	0-10
*45. Insertion of metasoma	10	10	always 10
46. Metasomal petiole	2	2	always 2
*47. Basal carina on S1	2.13	2	1-3
48. Shape of sternum 2	6.67	4	4-10
*49. Lateral line on T1	2.75	3	1-3
50. Male metasomal segments	10	10	always 10
51. Female pygidial plate	0.67	1	0-1
52. Female sternum 6	7.78	10	5-10
53. Apex of female metasoma	0	0	always 0

54. Male cerci	0.33	0	0-1
55. Male tergum 7	7.78	10	0-10
56. Volsella	1	1	always 1
57. Teeth on penis valves	4.11	3	1-10
58. Apex of marginal cell	0	0	always 0
59. Submarginal cells	0.44	0	0-1
60. Forewing vein 3rs-m	0	0	always 0
*61. Forewing vein 2-Rs	0.38	0	0-1
62. Number of discoidal cells	10	10	always 10
*63. Forewing vein M	6.75	10	1-10
64. First submarginal cell	4	4	always 4
65. Vein Rs + M	10	10	always 10
*66. Jugal lobe	1.25	1	0-3
*67. Hind wing vein 2A	2.50	2	2-4
*68. Hind wing vein 3A	5.13	3	1-10
69. Plumose hairs	10	10	always 10
70. Female tergum 7	10	10	always 10
71. Female hind basitarsus	10	10	always 10
72. Larval provisions	10	10	always 10
73. Pronotum (posterolateral)	10	10	always 10
74. Pronotum (ventral angle)	10	10	always 10
75. Metapostnotum	10	10	always 10
*76. Hindtibial strigilus	2.25	2	2-4
77. Pronotum (hind margin)	10	10	always 10
78. Prosternum	10	10	always 10
79. Larval integument	7.20	10	3-10
80. Larval body shape	4	4	always 4
81. Position of larval anus	7.60	10	4-10
82. Larval spiracles	5.20	4	4-10
83. Larval parietal bands	1.80	2	1-2
84. Larval antennal papillae	1.80	2	1-2
85. Larval mandibles	3.20	3	2-4
86. Larval maxillae	3.60	4	2-4
87. Larval galea	6.40	4	4-10
88. Larval spinnerets	5	5	always 5
89. Male sternum 7	2.11	2	1-4

Autapomorphies of Apoidea: 18, 73, 74, 75, 77
Autapomorphies of terminal taxa: 8 (Palarini), 23 (Oxybelini), 36 (Oxybelini), 65 (Oxybelini)

phylogenetic hypothesis will reveal which characters support that hypothesis and which do not. As in any scientific investigation, further analysis can then be done to try to reconcile the conflicting evidence from the initial study.

It is also worth remembering that the groundplan states assigned to the hypothetical ancestor by the analytical procedure developed by Maddison et al. (1984) depend upon the validity of the phylogenetic hypothesis derived from the work of Brothers (1975) and Carpenter (1990). This is more than a trivial truism because the procedures that Brothers used to polarize characters in his analysis were, insofar as one can judge from his paper, essentially the same as those employed by Bohart and Menke. One respect in which his outgroup comparisons

may have differed from those of Bohart and Menke and Evans is that he seems to have placed special emphasis on a putative sister group of the Aculeata, the family Trigonalysidae (Brothers 1975 p. 491). The analyses presented in this paper show how sensitive phylogenetic hypotheses can be to polarity decisions for only a few characters in a data set, if that data set has high levels of character conflict. Until cladistic relationships among the major hymenopteran lineages are more completely understood, assigning groundplan character states for the Apoidea will remain problematic. This, in turn, will contribute to the difficulty of determining cladistic relationships within the Apoidea.

In my opinion, it is premature to propose any changes in the higher level classification of Apoidea on the basis of these analyses. I have nothing substantive to add to the long-standing debate about the merits of phenetic, cladistic, and more traditional classifications that attempt to combine cladistic and phenetic information. However, I will state for the record my preference for strictly cladistic classifications, in which only monophyletic (or holophyletic) groups are recognized and there is a direct correspondence between the classification and the branching pattern of phylogeny. Lomholdt's (1982) classification of sphecids wasps and bees is the only one known to me that has had these goals, but the analyses described in the present paper do not support the phylogenetic hypothesis upon which Lomholdt's classification is based. Indeed, my analyses demonstrate that no well-corroborated phylogenetic hypothesis for the sphecids wasps is yet available, so the necessary framework for a stable cladistic classification is also not yet available.

I do not consider the development of a sound phylogenetic hypothesis to be an unattainable goal, but the type of character analysis necessary to achieve this goal remains to be done. The major utility that I see for the analyses presented here is that they provide a starting point for studies aimed at developing a more rigorously formulated and more stable phylogenetic hypothesis upon which to base a classification. In particular, where monophyletic assemblages of tribes can be identified (Table 7), one can proceed to study relationships within these groups. For example, I have done such an analysis at the genus level for the "Philanthinae *sensu stricto*" of Table 7 (Alexander, 1992). Long-recognized groups whose monophyly is not supported by the evidence considered in this

paper (see Table 8) should be examined to determine if evidence for their monophyly has been overlooked or misinterpreted.

A long-standing and conspicuous disagreement about the higher level classification of sphecids wasps and bees centers upon the issue of which taxa should be assigned the rank of family (for example, compare Bohart and Menke 1976 with Krombein 1979). Cladists and evolutionary taxonomists use different criteria to resolve questions about taxonomic rank, and I will restrict myself to a consideration of rank from a cladistic perspective. Taxonomic rank in a cladistic classification simply indicates position in a branching sequence, and does not imply anything about overall phenetic similarity among taxa sharing the same rank. In a cladistic classification, a single family Sphecidae comprising all the Apoidea that are not bees is unacceptable, because it is clearly a paraphyletic group. If it could be shown that all of the taxa recognized as subfamilies in Bohart and Menke's classification are monophyletic, and that they are arrayed in a perfectly pinnate branching sequence, each taxon could be assigned the rank of family according to the sequencing convention of Nelson (1972). A different type of branching pattern would require a different combination of families and subfamilies. However, with our present dim understanding of phylogenetic relationships, it is unclear which of the groups of sphecids wasps that some recognize as families and others as subfamilies are even monophyletic, let alone what branching pattern links monophyletic groups. Tables 7 and 8 indicate that the evidence regarding the monophyly of these groups is mixed. From a cladistic perspective, the "one family vs. many families" debate over sphecids wasps amounts to a choice between a single family Sphecidae that is clearly paraphyletic or a mixed assemblage of smaller families, of which some are probably monophyletic and others not. The monophyly of bees is strongly supported, but the appropriate rank to assign them in a cladistic classification depends upon the branching pattern among the Apoidea that are not bees. This is not a satisfactory situation. It is a problem that needs to be addressed, if our classification is to serve as a powerful analytical tool rather than a source of confusion in our attempts to understand these beautiful and fascinating insects.

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- CHRYSIDOIDEA**
- Plumariidae:** *Plumaroides andalgalensis*, *Plumarius* sp., *Myrmecopterina* sp.
- Bethylidae:** *Epyris coriaceus*, *E. clarimontis*, *Anisepyrus aurichalcus*, *A. subviolaceus*, *Pristocerus armifera*
- Scolebythidae:** *Clystospenella longiventris*
- VESPOIDEA**
- Sierolomorphidae:** *Sierolomorpha ambigua*, *S. canadensis*, *S. nigrescens*, *S. similis*
- Rhopalosomatidae:** *Rhopalosoma nearcticus*, *Olixon banksii*
- Pompilidae:** *Auplopus (Lophogenia) erigone*, *Episyrus biguttata*, *Priocnemoides fulvicornis*
- Anthoboscinae:** *Lalapa lusa*, *Plesiomorpha albinervis*, *Cosila chilensis*, *Anthobosca madecassa*
- INGROUP**
- Andrenidae:** *Andrena thaspii*, *Calliopsis andreniformis*
- Halictidae:** *Halictus rubicundus*, *Augochlora pura*, *Dufourea marginata*, *Nomia notiomorpha*
- Melittidae:** *Melitta leporina*
- Colletidae:** *Hylaeus basalis*, *Colletes wootoni*
- Anthophoridae:** *Exomalopsis albata*
- Megachilidae:** *Ashmeadiella californica*, *Megachile texana*
- Ampulicini:** *Ampulex canaliculata*
- Dolichurini:** *Dolichurus corniculatus*
- Sceliphriini:** *Sceliphron caementarium*, *S. assimile*, *S. spirifex*, *Chalybion californicum*, *Chlorion aerarium*, *Podium rufipes*, *P. flacipenne*, *P. luctuosum*
- Sphecini:** *Prionyx atratus*, *P. thomae*, *Isodontia mexicana*, *I. philadelphia*, *I. auripes*, *I. elegans*, *Palmodes dimidiatus*, *Sphex ichneumoneus*, *S. pensylvanicus*, *S. argentatus*, *S. tepanecus*
- Ammophiliini:** *Podalonia luctuosa*, *P. tydei*, *P. robusta*, *Ammophila procer*, *A. urnaria*, *A. harti*, *A. juncea*, *A. campestris*, *A. aberti*, *A. placida*, *A. pruinosa*, *A. fernaldi*
- Dinetini:** *Dinetus pictus*
- Astatini:** *Astata unicolor*, *A. occidentalis*, *A. minor*, *A. boops*, *A. bicolor*, *Dryadella immigrans*
- Palariini:** *Palarus variegatus*
- Miscophini:** *Miscophus bicolor*, *M. (Niteloapterus) evansi*, *M. (N.) slossonae barberi*, *Nitela spinolae*, *Plenoculus davisii*, *Solierella blaisdelli*, *S. peckhami*, *S. compedita*
- Larrini:** *Ancistromma distincta*, *Liris haemorrhoidalis*, *Li. nigra*, *Larra analis*, *La. luzonensis*, *Tachytes aurulentus*, *T. crassus*, *T. distinctus*, *T. mergus*, *Tachysphex apicalis*, *Tx. costa*, *Tx. obscuripennis*, *Tx. nitidus*, *Tx. pompiliformis*
- Trypoxylini:** *Pisonopsis birkmanni*, *Pison argentatum*, *P. atrum*, *Trypoxylon (Trypargilum) clavatum*, *T. (Tg.) collinum*, *T. (Tg.) politum*, *T. (Tg.) spinosum*, *T. (Tg.) tridentatum*, *T. (Tg.) texense*, *Trypoxylon (Trypoxylon) ashmeadi*, *T. (Tn.) figulus*, *T. (Tn.) frigidum*, *T. (Tn.) johnsoni*
- Crabronini:** *Anacrabro ocellatus*, *Crabro advenus*, *Cb. argusinus*, *Cb. monticola*, *Crossocerus ammulipes*, *Cs. capitatus*, *Cs. cinxius*, *Cs. fergusonii*, *Cs. nigratus*, *Cs. podagritus*, *Cs. quadrimaculatus*, *Cs. walkeri*, *Ectemnius atriceps*, *E. cavifrons*, *E. continuus*, *E. guttatus*, *E. paucimaculatus*, *E. sexcinctus*, *E. stirpicolus*, *E. tumidiventris*, *E. zonatus*, *Entomognathus brevis*, *Lindenius pygmaeus*, *L. tylosis*, *Moniaecera asperata*, *Rhopalum clazipes*, *R. coarctatum*, *R. pedicellatum*, *R. rufigaster*, *Tracheliodes amu*, *T. quinquenotatus*
- Oxybelini:** *Oxybelus argentatus*, *O. bipunctatus*, *O. quadrinotatus*, *O. victor*

APPENDIX 1: TAXA EXAMINED

For the ingroup, species selected for studies of adult morphology were those used in Evans' studies of sphecids larvae, plus exemplars from tribes whose larvae have never been described.

OUTGROUP

ICHNEUMONOIDEA

Ichneumonidae: *Existes roborator*, *E. comstockii*, *Pimpla aequalis*, *Scambus brevicornis*

Braconidae: *Doryctes* spp., *Spathius* spp., *Helcon* spp.

Bothynostethini: *Bothynostethus distinctus*, *Willinkia argentina*

Scaphetini: *Bohartella scapheutoides*, *Scapheutes brasiliensis*

Laphyragogini: *Laphyragogus pictus*

Xenosphecini: *Xenosphechus timberlakei*, *X. xerophilus*

Entomosericini: *Entomosericus concinnus*, *E. kaufmanni*

Heliocaasini: *Heliocaasus argentinus*, *H. fiebrigii*

Pemphredonini: *Ammoplanus handlirshi*, *Arpactophilus steindachneri*, *Diodontus minutus*, *D. tristis*, *D. virginianus*, *Microstigmus comes*, *Passalococcus clypealis*, *Pa. corniger*, *Pa. cuspidatus*, *Pa. eremita*, *Pa. gracilis*, *Pa. insignis*, *Pa. pictus*, *Pa. singularis*, *Pemphredon (Cemonus) gennelli*, *Pe. (C.) inornatus*, *Pe. (C.) lethifer*, *Pe. (C.) rugifer*, *Pe. (C.) wesmaeli*, *Pe. (Ceratophorus) morio*, *Pe. (Pemphredon) concolor*, *Pe. (P.) lugens*, *Pe. (P.) lugubris*, *Spilomena enslini*, *Stigmus fraternus*, *St. inordinatus*, *St. pendulus*, *St. solskyi*

Psenini: *Mimesa bicolor*, *Mimumesa nigra*, *Pluto albifacies*, *Psen ater*, *Psen bakeri*, *Psen simplicicornis*, *Psenulus fuscipennis*, *Psenulus pallipes*

Mellinini: *Mellinus arvensis*

Alyssonini: *Alysson melleus*, *A. cameroni*, *Didineis latimana*

Nyssonini: *Epinysson basilaris*, *Nysson daeckii*, *N. trimaculatus*

Gorytini: *Gorytes canaliculatus*, *G. pleuripunctatus*, *Hoplisoides costalis*, *H. hamatus*, *H. placidus*, *nebulosus*, *Ochleroptera bipunctata*, *Oryttus gracilis*, *Sphecius speciosus*

Stizini: *Bembecinus mexicanus*, *B. neglectus*, *B. tridens*, *B. quinquepinus*, *Stizoides uncinatus*, *Stizus pulcherrimus*

Bembicini: *Bembix amoena*, *B. beltragei*, *B. cameroni*, *B. cinerea*, *B. comata*, *B. hinei*, *B. integra*, *B. multipicta*, *B. nubilipennis*, *B. occidentalis*, *B. oculata*, *B. olivacea*, *B. pallidipicta*, *B. sayi*, *B. spinolae*, *B. texana*, *B. troglodytes*, *B. dentilabris*, *Bicyrtes fodiens*, *B. quadrifasciata*, *B. ventralis*, *Glenostictia pulla*, *G. scitula*, *Microbembex monodonta*, *Rubrica nasuta*, *Steniolia duplicata*, *S. elegans*, *S. longirostris*, *S. obliqua*, *Stictiella formosa*, *S. pulchella*, *S. serrata*, *Stictia carolina*, *S. heros*, *S. signata*, *S. vivida*

Eremiasphecini: *Eremiasphecium desertorum*, *E. schmidkecknehti*

Odontosphecini: *Odontosphechus paradoxus*

Pseudocoliini: *Pseudocolia dewitzi*, *P. pharaonum*, *P. theryi*, *P. tricolor*

Aphilanthopini: *Aphilanthops foxi*, *A. frigidus*, *A. hispidus*, *A. subfrigidus*, *Clypeadon bechteli*, *C. californicus*, *C. dreisbachi*, *C. evansi*, *C. haigi*, *C. laticinctus*, *C. sculleni*, *C. taurulus*, *C. utahensis*, *Philanthinus integer*, *P. quattuordecimpunctatus*

Philanthini: *Philanthus albopilosus*, *P. barbiger*, *P. bicinctus*, *P. bilunatus*, *P. coarctatus*, *P. coronatus*, *P. crabroniformis*, *P. gibbosus*, *P. politus*, *P. solivagus*, *P. triangulum*, *Trachypus mexicanus*, *T. petiolatus*

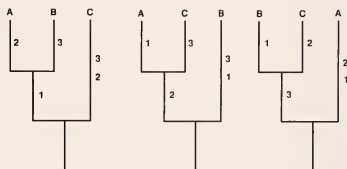
Cercerini: *Cerceris angularis*, *C. clypeata*, *C. flavofasciata floridensis*, *C. frontata frontata*, *C. fumipennis*, *C. nigrescens*, *C. robertsoni robertsoni*, *C. r. emmitosus*, *C. rubida julii*, *C. sabulosa*, *C. quinquefasciata*, *Eucerceris bitruncata*, *E. flavocincta*

Heterogyna: *H. botswana*, *H. fantsilotra*, *H. madecassa*, *H. protea*

APPENDIX 2

On a strict consensus tree, polytomies usually mean that there are numerous equally parsimonious arrangements of the taxa involved in the polytomy. This creates difficulties for one wishing to present the evidential support for a consensus tree by mapping the distribution of character states upon the tree. It has even been argued that character states should not be mapped onto consensus trees (Nixon 1991). The following simple example is intended to explain how one might interpret the distributions of character states on the polytomies in the consensus trees in this paper. The simplest possible polytomy would involve three taxa and three characters. There are three possible cladograms for three taxa, and in this example each of the possible trees is supported by one character (a "1" in the data matrix represents the apomorphic character state). A strict consensus tree for this data set would be an unresolved trichotomy. The cladograms show how characters are distributed on each of the three equally parsimonious cladograms (all three cladograms have a length of 5 steps). If characters are mapped onto the strict consensus tree, each terminal taxon is depicted as having two autapomorphies, whereas in each of the fully resolved cladograms only one terminal taxon has two autapomorphies. In general, whenever two or more taxa involved in a polytomy on a consensus tree share a derived character state, that character state can be interpreted as a synapomorphy in one or more of the equally parsimonious cladograms that are represented by the polytomy. For example, characters 13, 14, and 15 in Fig. 1A are depicted as autapomorphies for the taxa *Aphilanthopini*, *Philanthini*, and *Cercerini*. Fig. 1A is a consensus tree for 5,272 equally parsimonious cladograms, and on many of these cladograms characters 13-15 would be synapomorphies for a monophyletic group containing the tribes *Aphilanthopini*, *Philanthini*, and *Cercerini*.

TAXON	CHARACTER		
	1	2	3
A	1	1	0
B	1	0	1
C	0	1	1



THREE EQUALLY PARSIMONIOUS CLADGRAMS



STRICT CONSENSUS TREE

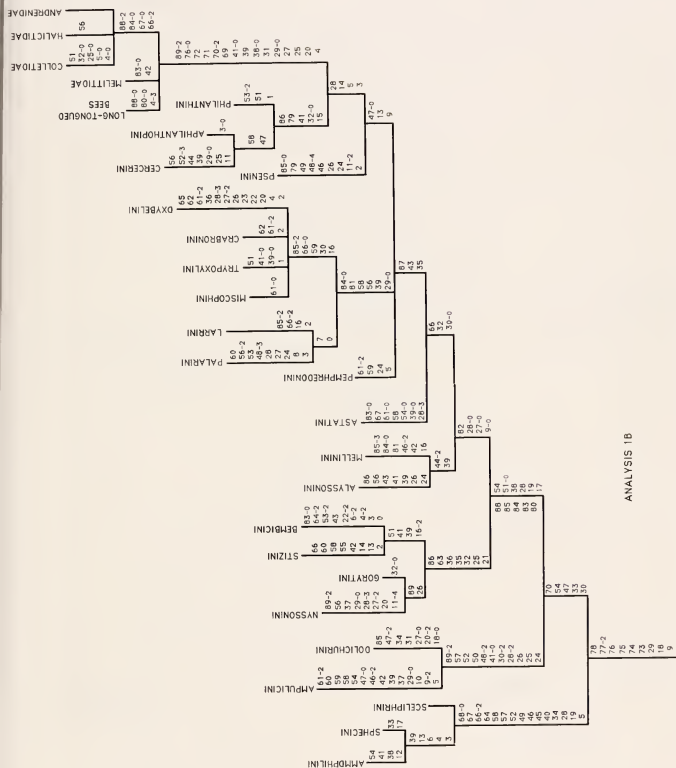
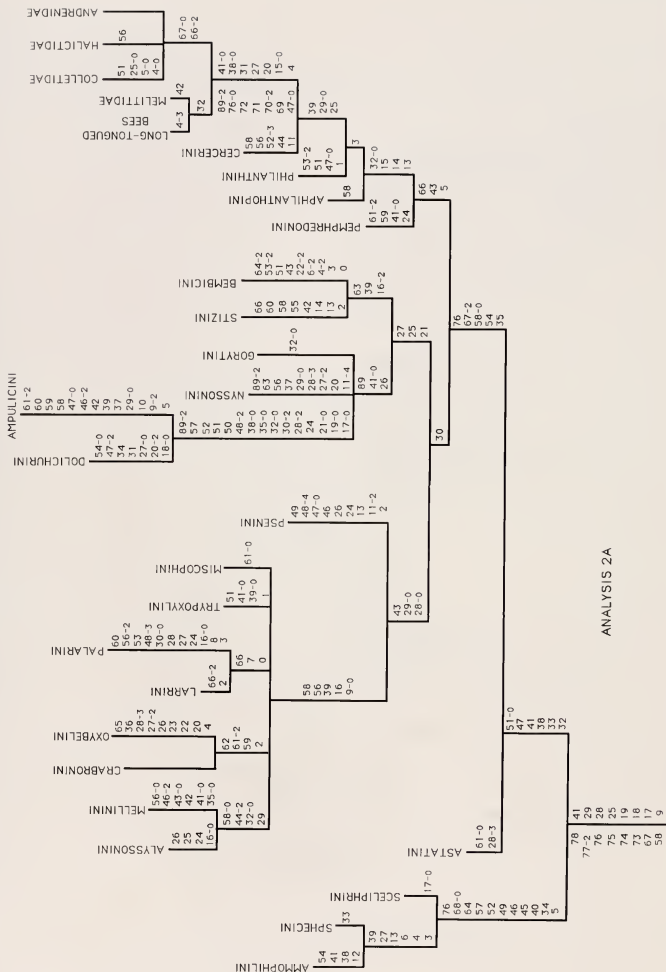


Fig. 1. Strict consensus tree for Analysis 1 (adult and larval characters, tribes with unknown larvae excluded, polarities taken from the literature); (A) equal weights for all characters, (B) successive approximations character weighting. In Figs. 1-10, numbers on the branches correspond to the characters in Tables 1 and 2. Where a character number is shown without a subscript, it is implicitly hypothesized that a transition from state 0 to state 1 has occurred. Other character state transitions are identified by appropriate subscripts. Characters are not mapped on branches where more than one state may occur, either because more than one state would be equally parsimonious for a hypothetical ancestor, or because the character is coded as variable for a terminal taxon.



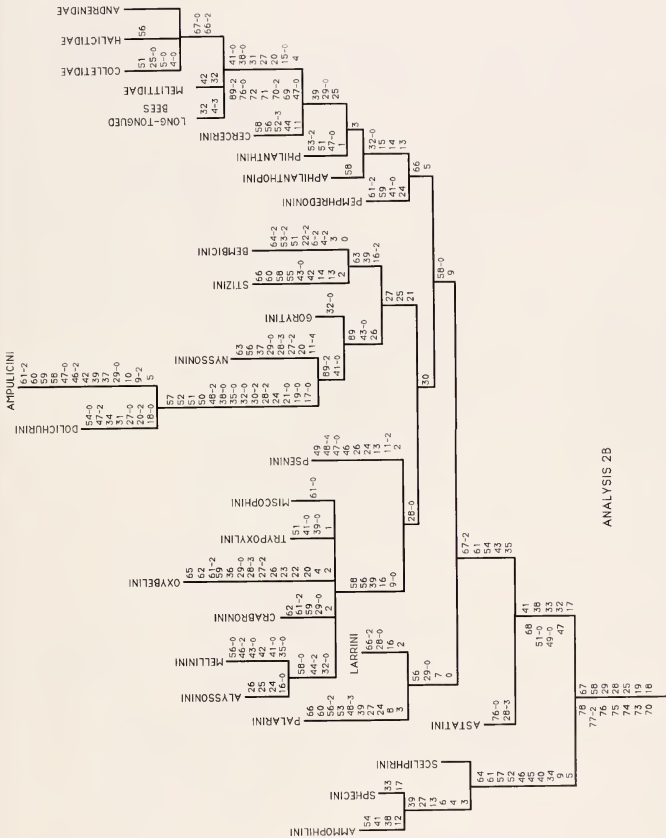


Fig. 2. Strict consensus tree for Analysis 2 (adult characters only, tribes with unknown larvae excluded, polarities taken from the literature); (A) equal weights for all characters; (B) successive approximations character weighting.

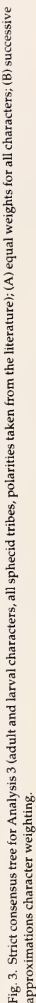


Fig. 3. Strict consensus tree for Analysis 3 (adult and larval characters, all spicid tribes, polarities taken from the literature); (A) equal weights for all characters; (B) successive approximations character weighting.

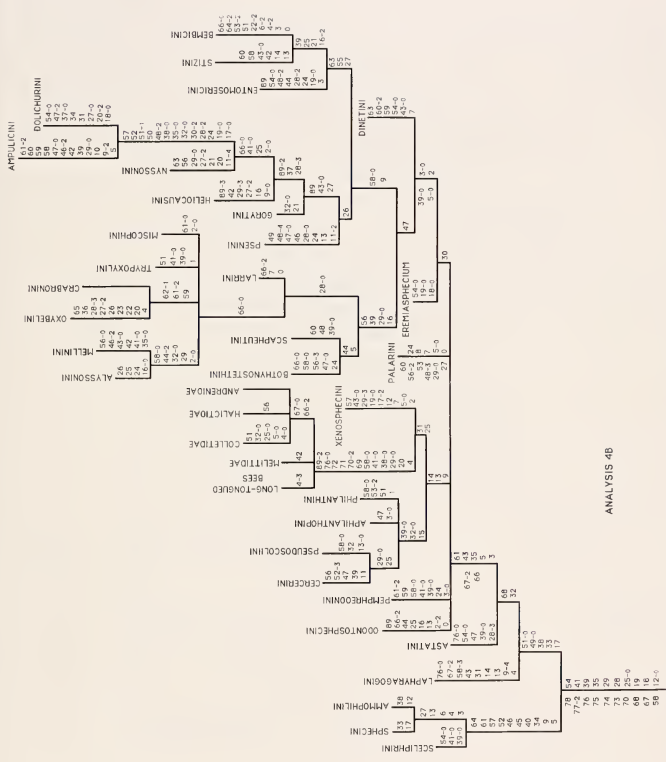


Fig. 4. Strict consensus tree for Analysis 4 (adult characters only, all species tribes, polarities taken from the literature); (A) equal weights for all characters; (B) successive approximations character weighting.

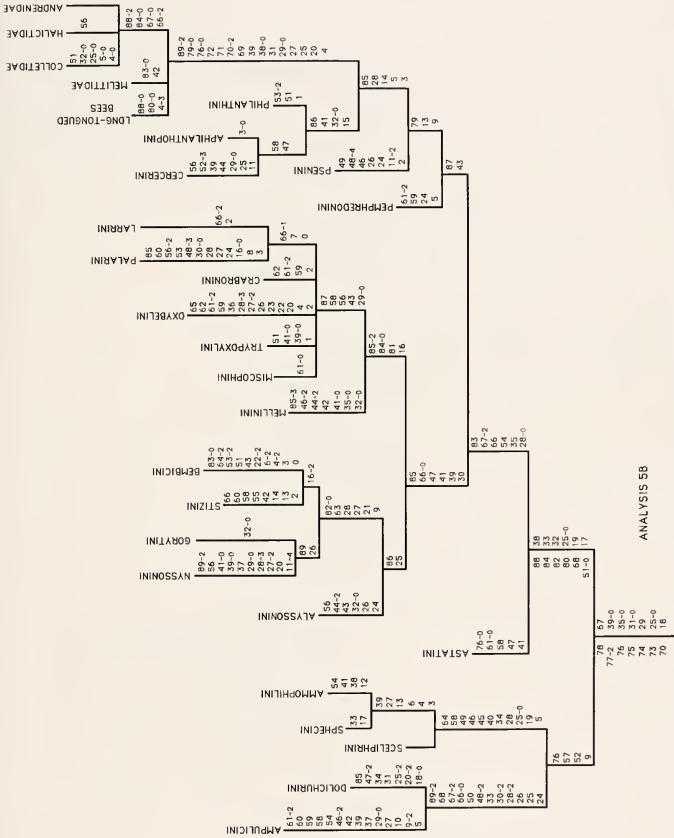
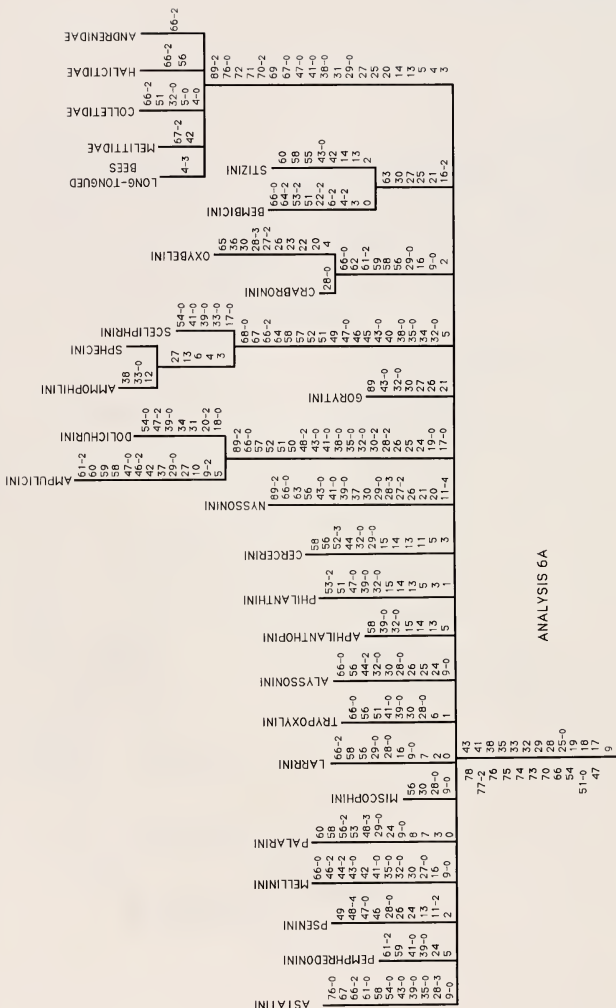


Fig. 5. Strict consensus tree for Analysis 5 (adult and larval characters, tribes with unknown larvae excluded, polarities based on optimization). (A) equal weights for all characters, (B) successive approximations character weighting.



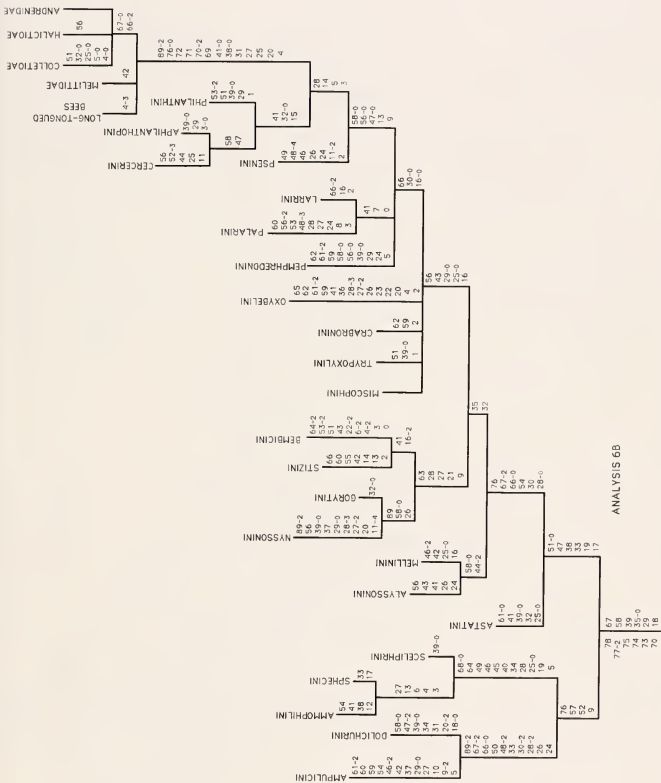
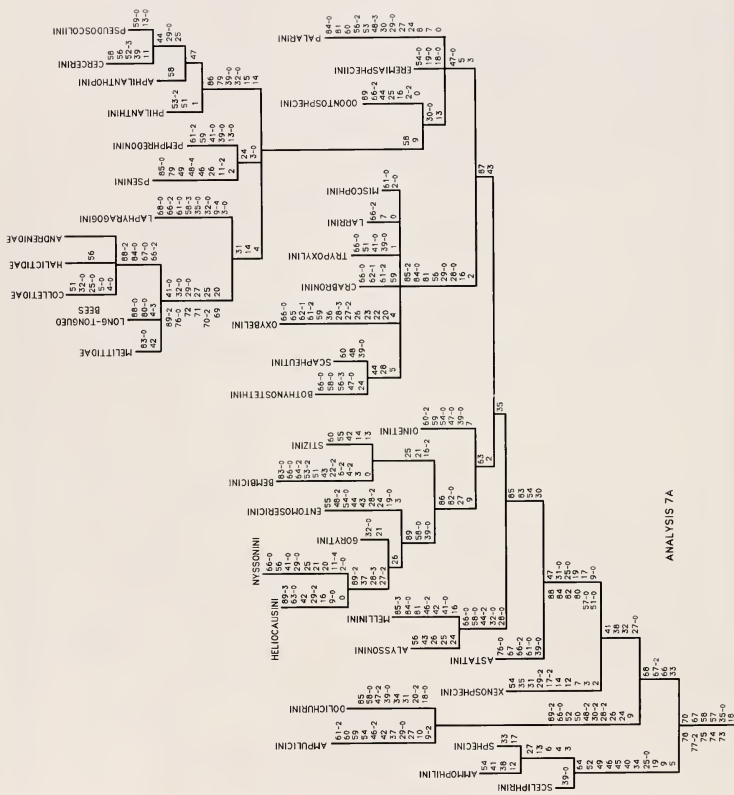


Fig. 6. Strict consensus tree for Analysis 6 (adult characters only, tribes with unknown larvae excluded, polarities based on optimization); (A) equal weights for all characters; (B) successive approximations character weighting.



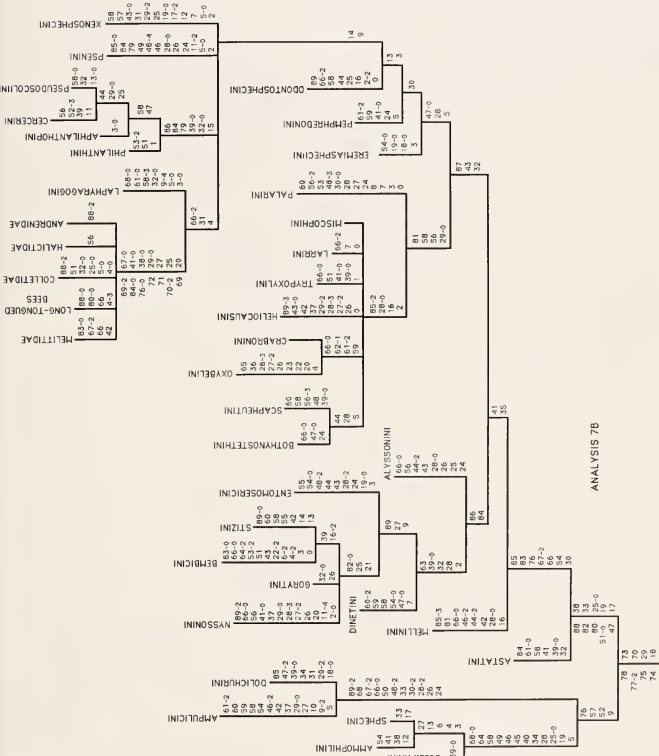


Fig. 7. Strict consensus tree for Analysis 7 (adult and larval characters, all sphecoid tribes, polarities based on optimization); (A) equal weights for all characters; (B) successive approximations character weighting.

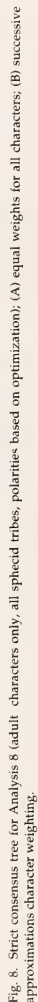


Fig. 8. Strict consensus tree for Analysis 8 (adult characters only, all aphecid tribes, polarities based on optimization); (A) equal weights for all characters; (B) successive approximations character weighting.

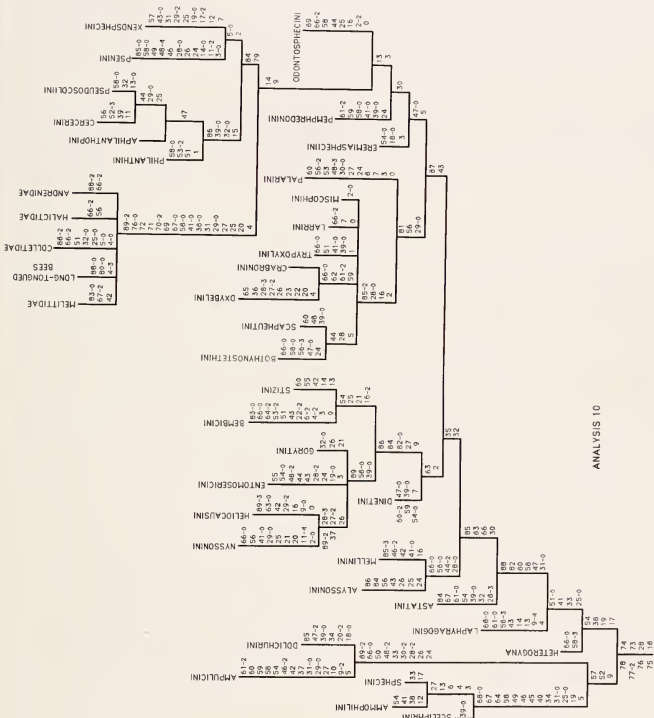


Fig. 10. Strict consensus tree for an analysis that included the genus *Heterogyna* (adult and larval characters, all sphecoid tribes, polarities based on optimization, successive approximations character weighting).

The Application of Nucleotide Sequence Data to Phylogeny of the Hymenoptera: A Review

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Abstract.—The application of molecular sequence data to studies on the phylogeny of the Hymenoptera are reviewed, with special attention given to the relationships among the higher levels of the Order. Methods for obtaining sequence information from nuclear-encoded ribosomal RNA (rRNA) and mitochondrial rRNA and protein-coding genes are described. Techniques for alignment and phylogenetic analysis of sequences are discussed, as are issues associated with the selection of outgroups. Recent molecular investigations of hymenopteran phylogeny at several taxonomic levels are discussed to illustrate the application of methods and analytical procedures.

The use of DNA sequence data for systematics is recent and controversial. The controversies are not about whether nucleotide sequences are appropriate for reconstructing phylogenetic history but rather, how they should be used. Therefore, the springboard for our review is not a justification of the relative merits of sequence data over the application of other techniques for phylogenetic analysis (for this see Hillis and Moritz 1990), instead we begin with a discussion of the areas of controversy that have arisen with the use of DNA sequences for phylogenetic analysis. We review each of these issues and make recommendations based in part on our own experiences with collecting and analyzing DNA sequences of Hymenoptera.

Differences of opinion have arisen over aspects of sequence data collection and analysis, including (1) the appropriate genes (or gene fragments) to be sequenced and their use for different levels of inference; (2) methods of data acquisition; (3) methods of alignment, character weighting, and tree-building; (4) assumptions (or the lack thereof) of the models of nucleotide evolution; (5) consideration of molecular secondary structure and the degree to which it can bias interpretation of sequence data for phylogenetic reconstruction; and (6) appropriate statistical analyses for estimating the reliability of molecular phylogenies. Each of these issues confronts all systematists who wish to approach phylogenetic reconstruction from a mo-

lecular perspective, altogether a non-trivial pursuit for beginner and experienced alike.

This paper arose from the symposium 'Phylogeny of the Hymenoptera', which was featured during the 2nd Quadrennial meeting of the International Society of Hymenopterists, held in August, 1991 in Sheffield, England. Three contributions in the symposium presented results of phylogenetic analyses using DNA sequences. It became clear at this meeting that many of our audience were unfamiliar with the use of sequence data for systematic studies. In the future, systematists will have to interpret critically the results from molecular studies in order to compare them effectively with their own investigations based on morphology or other types of data. Therefore, we thought it worthwhile to review the subject of molecular phylogeny with particular reference to the Hymenoptera. To remain faithful to the theme of the symposium, we primarily restrict our discussion in this review to questions of higher level phylogeny, that is, to the tribal level or above. However, we include a single study of relationships at the species level. Given that little has been published on comparative DNA sequences for phylogenetic reconstruction of the Hymenoptera (but see Cameron 1991; Garnery et al. 1991; Sheppard and McPherson 1991), we rely heavily on our own investigations of sequence comparisons of the small (18S) subunit ribosomal RNA gene (rRNA) and the large (16S) rRNA gene encoded by the mitochondrial genome (mtDNA). For a general review of the field of molecular systematics we recommend two

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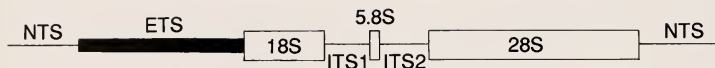


Fig. 1. Generalized diagram illustrating the components of the nuclear rRNA repeat unit (in this case that of vertebrates, after Gerbi 1985), showing the relative positions of the 5.8S, 18S and 28S regions, nontranscribed spacers (NTS), an external transcribed spacer (ETS) and two internal transcribed spacers (ITS).

excellent books by Hillis and Moritz (1990) and Miyamoto and Cracraft (1991); for reviews of molecular techniques and applications for insect systematics see Simon (1991) and Simon et al. (1990, 1991). Ladiges and Martinelli (1990), though focusing on plant systematics, also contains a number of useful general papers on both theoretical and practical aspects of molecular systematics.

CLASSES OF DNA FOR PHYLOGENETIC ANALYSIS

In the last decade, the application of molecular data to systematics has expanded enormously, and comparative DNA sequences have become the preferred data for such investigations (Hillis and Moritz 1990; Miyamoto and Cracraft 1991). Sequence characters from nuclear and extranuclear genomes offer a more or less unlimited supply of diverse characters applicable for analyses at all taxonomic levels, from the population to the Kingdom. Different genes and gene regions exhibit vastly different evolutionary rates, structural or functional constraints, and mutational biases (Nei 1987; Larson and Wilson 1989; Simon et al. 1991), thus it is potentially possible to match specific systematic questions to appropriate genomic regions for analysis. For example, regions of DNA that are evolutionarily conserved, such as sections of rRNA (Gerbi 1985), are useful for resolving early phylogenetic history (Field et al. 1988; Lake 1988; Mindell and Honeycutt 1990), whereas regions showing intermediate (Larson and Wilson 1989) or rapid divergence (Brown et al. 1979; Crozier et al. 1989) are useful for evaluating evolutionary events that occur on intermediate (Larson 1991; Cameron 1991) or short (Greenberg et al. 1983) time scales. Nuclear rRNA sequences have been used extensively for the phylogenetic reconstruction of a great diversity of organisms, and more recently, mitochondrial rRNA and protein-coding genes have contributed even more sequence information (Simon et al. 1991). We briefly review each of these

classes of DNA.

Nuclear encoded rRNA.—Ribosomes are the sites for cellular protein synthesis and as such their RNA is present in many copies and is abundant compared with cellular mRNA and tRNA. Eukaryote rRNA is composed of two subunits; the smaller subunit has a sediment coefficient of about 18 and is known as 18S rRNA, while the larger subunit comprises three components, viz. 5S, 5.8S and 28S rRNA (Fig. 1). Sequences from the smaller components (5S and 5.8S) are generally inappropriate for phylogenetic analysis because of their size, but the intermediate and larger subunits, particularly 18S rRNA, have been used to examine relationships among a great range of taxa (Johnson and Baverstock 1989; Mindell and Honeycutt 1990; Baverstock and Johnson 1990; Larson 1991). The 18S rRNA is 1700 to 2300 bases long in eukaryotes and as a non-coding region, its insertions and deletions can comprise any number of bases (not limited to multiples of three) because frame shifts do not apply. Furthermore, comparison of sequences indicates that introns are generally absent in rRNA (Baverstock and Johnson 1990).

Some regions of 18S rRNA are moderately variable and have application for lower levels of phylogenetic analysis. However, the more conserved regions have been the focus of many higher-level studies. Indeed, so called 'fossil RNA' exhibits identical sequences (24 bases in length) between organisms as divergent as prokaryotes (e.g., archaeobacteria) and eukaryotes (e.g., humans). Generally, 18S rRNA sequences are considered useful for taxa that diverged from 100-1000 Mya (Baverstock and Johnson 1990), while 28S rRNA sequences are useful for divergent times of 60-200 Mya (Larson 1991). Studies to date (Table 1) have examined the relationships between Kingdoms, major prokaryote groupings, protistan phyla, invertebrate phyla, classes of platyhelminths, chordate groups, and vertebrates. Few studies have been published on the phylogeny of insect groups

Table 1. Selected references to studies employing rRNA sequence data for phylogenetic analysis and the corresponding taxa examined.

Reference	Region	Taxon
Nuclear 5S, 5.8S, 18S and 28S rRNA		
Walker 1985	5S & 5.8S	Protistan phyla
Woese et al. 1990	18S	Kingdoms
Fox et al. 1980	18S	Major prokaryote groups
Woese 1987	18S	Major prokaryote groups
Johnson & Baverstock 1989 (review)	18	Protistan phyla
Field et al. 1988	18S	Invertebrate phyla
Baverstock et al. 1991a	18S	Platyhelminths
Qu et al. 1986	18S	Helminths
Wheeler 1989	18S	Insect orders
Joss et al. 1991	18S	Chordate groups
Baverstock et al. 1991b	18S	Higher vertebrates
Jupe et al. 1988	18S	Algae
Mindell & Honeycutt 1989	18S/28S	Birds
Hedges et al. 1990	18S/28S	Tetrapods
Hamby & Zimmer 1988	18S/26S	Grasses
Zimmer et al. 1989	18S/26S	Flowering plants
Baroin et al. 1988	28S	Unicellular eukaryotes
Vossbrinck & Friedman 1989	28S	Diptera
Larson 1991	28S	Salamander
Hillis & Dixon 1989	28S	Vertebrates
Hillis & Davis 1987	28S	Amphibians
Schmickel et al. 1990	28S	Primates
Sheppard & McPheron 1991	18S/28S	Apidae
Nuclear intergenic spacer (IGS) of rRNA		
Collins et al. 1987	-	<i>Anopheles</i> (Diptera)
Beach et al. 1989	-	<i>Anopheles</i> (Diptera)
Collins et al. 1989	-	<i>Anopheles</i> (Diptera)
Tautz et al. 1987	-	<i>Drosophila</i> (Diptera)
Lassner et al. 1987	-	<i>Triticum</i> (wheat)
Sheppard & McPheron 1991	ITS1	Apidae
Mitochondrial 12S and 16S rRNA		
Cameron 1991	16S	Apidae
Derr et al., in press	16S	Hymenoptera
Thomas et al. 1989	12S	marsupials
Hixson & Brown 1986	12S	primates
Miyamoto & Boyle 1989	12S/16S	eutherian mammals
Miyamoto et al. 1989	12S/16S	artiodactyl mammals
Simon et al. 1990	12S	cicadas
Sheppard & McPheron 1991	12S (very divergent)	Apidae

using nuclear encoded rRNA sequences; exceptions include Vossbrinck and Friedman (1989) on cyclorrhaphous Diptera, Wheeler (1989) on the Insecta, Sheppard and McPheron (1991) on Apidae. Also, a recent analysis of the blattoid insects has been completed by Vawter (1991 Ph.D. dissertation).

Mitochondrial DNA.— Animal mtDNA is a circular, double-stranded molecule ranging from about 14 kb to 39 kb in length (reviewed in Avice et

al. 1987; Moritz et al. 1987). The mtDNA of only one insect, *Drosophila yakuba*, has been completely sequenced (Clary and Wolstenholme 1985). It encodes 13 proteins, 22 tRNAs and two rRNAs, as for most animals. Partial mtDNA sequences are known for other insects, including crickets (Rand and Harrison 1989), mosquitoes (HsuChen and Dubin 1984; HsuChen et al. 1984), cicadas (Simon et al. 1990), and honey bees (Vlasak et al. 1987; Crozier et al. 1989; Garnery et al. 1991; Cameron, unpublished data). For a complete list of published mtDNA sequences see Simon et al. (1991).

In vertebrates, mtDNA has been found to evolve many times faster than single-copy nuclear DNA (scnDNA) (Moritz et al. 1987), in contrast to invertebrates, which exhibit approximately equal rates of change (amino acid or nucleotide substitutions) for both genomes (Vawter and Brown 1986; Powell et al. 1986). In the Hymenoptera, some mtDNA genes are highly conserved (e.g. ND3, Les Willis, unpublished data for *Apis*), while others exhibit rapid rates of divergence (e.g., COII, Crozier et al. 1989; Garnery et al. 1991; rRNA, Cameron, unpublished data; Derr et al., in press). Within both the 12S and 16S rRNA genes, some regions are highly conserved while other regions are rapidly diverging (Cameron, unpublished data; Derr et al., in press). Recent investigations of honey bee mtDNA indicate that it has a significantly greater evolutionary rate than that of *Drosophila* (Crozier 1989); however the causal factors are unknown.

In summary, current knowledge suggests that hymenopteran mtDNA exhibits vastly different rates of evolution, and therefore is useful for phylogenetic inference at many levels. A note of caution, however, when examining relationships below the genus level. The random sorting of polymorphic genes within a species may lead to a lack of congruence between the phylogenetic pattern of the gene (mtDNA) and that of a group of closely related species (Takahata 1989). We discuss below (Examples of Current Research) the usefulness of comparative sequences from the 16S rRNA gene for assessing phylogenetic relationships at three different levels: (1) among species of the genus *Apis*, (2) among tribes of the family Apidae, and (3) among families and superfamilies of Hymenoptera.

Protein-coding genes.— Protein-coding genes (also referred to as structural genes) are transcribed into RNA and then translated into proteins. These have been used less often for phylogenetic analyses, in part because early on, rRNA genes (mito-

chondrial and nuclear) proved useful for many levels of phylogenetic inference (see above). Thus, a large number of rRNA primers have been synthesized, many of which are applied to new studies utilizing sequence data. Fewer primers are available for protein-coding genes. An additional concern is that many nuclear encoded protein-coding genes are parts of multiple-copy divergent gene families, making analysis (and possibly PCR) more complicated. However, the application of mitochondrial protein-coding sequences for phylogenetic studies of Hymenoptera is expanding. In addition to the study of *Apis* relationships by Garnery et al. (1991), full sequences are available for the mitochondrial COI and COII genes of *A. mellifera* L. (Crozier 1989). These have been used to synthesize primers for several current phylogenetic investigations, including another analysis of the genus *Apis* (Les Willis, unpublished data). For a review of current knowledge on mitochondrial protein-coding genes, including primer sequences used for PCR and sequencing, see Simon et al. (1991).

OBTAINING SEQUENCE DATA FOR PHYLOGENETIC ANALYSIS

Although the usefulness of nucleotide sequences for phylogenetic analysis has become widely recognized, the need for technical training in molecular biology, and the time and expense involved in obtaining the data has curtailed widespread use of the technology for systematics. This has been particularly true for Hymenoptera and other insect groups, which are small relative to vertebrates, presenting challenges for extracting DNA in sufficient quantities for sequencing. In addition, many Hymenoptera, especially aculeates, have a hard chitinous exoskeleton which, in contrast to the soft-bodied *Drosophila*, makes DNA extraction more difficult.

These problems have, in principle, been solved by the revolutionary new development of automated technology for the enzymatic amplification of DNA based on the polymerase chain reaction (PCR) (Saiki et al. 1988; Innis et al. 1990). PCR is a thermocyclic reaction (discussed below) that generates multiple copies of a fragment of DNA relatively quickly and cheaply, eliminating the lengthy procedures of viral or bacterial cloning (Saiki et al. 1985; Mullis et al. 1986; Mullis and Faloona 1987; Cherfas 1990; Innis et al. 1990; Mullis 1990). Although PCR is still in its infancy as a tool for

systematics, this method now makes it feasible to obtain large quantities of homologous DNA for direct sequencing from individual insects (Wheeler 1989; Simon et al. 1991; Cameron 1991). Because small amounts of template DNA are sufficient for amplification with PCR, samples no longer must be fresh or frozen, they may be preserved in alcohol or formalin, or even dried (Pääbo 1989; Pääbo 1990; Kocher et al. 1989). Thus, PCR has the capacity to expand phylogenetic investigations to include untapped temporal and geographic coverage of museum specimens.

PCR works with two oligonucleotide primers, which are short pieces of DNA in the range of 18-25 base pairs (bp) in length (see Appendix 1). Each primer is designed to be complementary to one of the two strands of the sample DNA, and together they flank the region to be amplified, which is usually several hundred to several thousand base pairs (kilobases or kb) in length. PCR occurs in three steps, repeated 30-40 times. First, the sample DNA is denatured by heat into its two respective strands. Next, the reaction mixture is cooled to allow the two primers to anneal to their complementary strands. Lastly, in the presence of a thermostable DNA polymerase, such as Taq polymerase (derived from a thermophilic bacterium), the two complementary sample strands are replicated by primer extension, beginning at the primer sites (for figured descriptions see Hillis et al. 1990; Simon et al. 1991). The target DNA is therefore replicated exponentially, and within several hours the double-stranded sample has been amplified several millionfold. Single-stranded DNA can be produced by using an excess of one of the primers, a procedure known as asymmetric amplification (Gyllenstein and Erlich 1988).

The procedures and protocols for DNA extraction, amplification, purification and sequencing (modified for Hymenoptera) are too extensive to present here and will be published elsewhere (Cameron, unpublished data; Derr et al., in press). However, several recent references provide useful information: Hillis et al. (1990) describe a basic laboratory setup, protocols, and recipes for stock solutions; Innis et al. (1990) provide a thorough description of PCR methodology and its various applications and protocols; Simon et al. (1991) provide up to date information on invertebrate mitochondrial (and other) primer sequences for use with PCR, as well as PCR protocols for use with insect taxa; and Maniatis et al. (1982) is an indis-

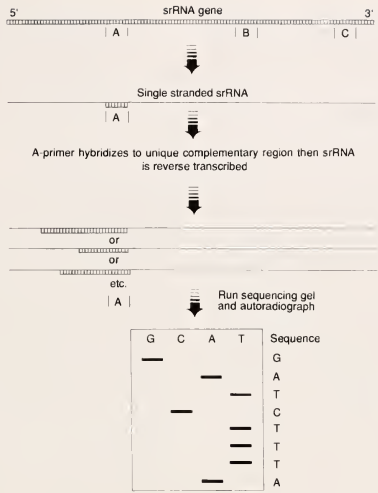


Fig. 2. Diagrammatic representation of the sequencing of small and large subunit rRNA using the reverse transcriptase method. In this case for the 18S rRNA, primer A is added to a bulk RNA extract; it hybridizes to the complementary region and acts to prime the initiation of DNA synthesis in a Sanger sequencing reaction (see text for further details) (after Johnson and Baverstock 1989).

pensable reference for many molecular procedures. Another method of obtaining DNA for sequencing is to isolate the transcribed DNA for a region of RNA (e.g., mRNA) and use reverse transcriptase for sequencing. This method, developed by Qu et al. (1983) and Lane et al. (1985) for obtaining sequences of RNA, provides a relatively quick and easy method of sequencing by using small conserved regions to prime reverse transcription of cellular RNA. In short, sample tissues are treated with guanidine hydrochloride to block RNAase activity. Bulk RNA, consisting primarily of rRNA, is then purified from DNA and protein (see Larson and Wilson 1989; Hillis et al. 1990). One of several oligonucleotide primers (e.g., Field et al. 1988; Baverstock et al. 1991a) is then added to the purified RNA and the DNA is then sequenced by chain termination (Sanger et al. 1977) at the same time that it is produced by reverse transcription. The resultant products are then run on a sequencing gel and the sequences read from an autoradiograph (Fig. 2). The entire procedure takes only days in-

stead of the months required for cloning DNA.

ANALYSIS OF SEQUENCE DATA

Sequence Comparison and Alignment.—Probably the most difficult and least understood aspect of the use of sequence data for phylogenetic analysis is sequence alignment (Swofford and Olsen 1990). Phylogenetic analysis of sequence information requires the correct alignment of homologous components between pairs of sequences. One must be careful to distinguish between phylogenetically homologous DNA sequences (orthologs) and multiple, diversified gene copies within single individuals (paralogs) (Fitch 1970, Patterson 1987). In phylogenetic studies, the goal is to compare orthologous sequences from taxa of interest. Superficially, this would seem a rather straightforward task. For example, each nucleotide position can be viewed as a 'character' with only a limited number of 'states' possible at each position (i.e., for DNA sequences, 'A', 'C', 'G', 'T', or a gap mutation

<u>Suborder</u>	<u>Superfamily</u>	<u>Genus</u>	<u>Nucleotide Sequence</u>
Symphyla	Siricoidea	<i>Tremex</i>	AA-ATATAAATTAAATTCT-
Apocrita	Vespoidea	<i>Polistes</i>	AA-AACATTTTAAATTCT-
Apocrita	Ichneumonoidea	<i>Xanthopimpla</i>	ATTAATA-AATTAAA-GCTC

Fig. 3. One possible sequence alignment from a small segment of the large ribosomal subunit (16S rRNA) of three representative hymenopterian taxa. This region corresponds to positions 13,205 to 13,225 of the published *Drosophila* sequence (Clary and Wolstenholme 1985) (data are from Derr et al., in press). From a total of 20 nucleotide positions from three taxa there are six inferred gap mutations, only six G or C bases, and 48 A or T bases. There are 10 possible base substitutions of which nine are transversions (involving A/T, A/C or G/T bases) and only one transition (T/C).

'-'). In practice, however, alignment of multiple nucleotide sequences can involve a number of complicating factors. For example, as discussed by Swofford and Olsen (1990), in addition to requiring the use of orthologous sequences, phylogenetic analysis of sequence data requires that one make the assumption that all nucleotides observed at a given position are traceable to a common ancestor. Historical events such as insertions, deletions, duplications, rearrangements, and multiple nucleotide substitutions all combine either to cloud the evolutionary history of some nucleotide positions or make non-homologous positions indistinguishable.

Determination of sequence homology and alignment usually presents few ambiguities when working with protein-coding gene sequences, particularly scdDNA. Landmark features along these sequences such as codons (three adjacent bases specifying an amino acid), intron/exon junction consensus sequences, various start and stop signals, and other DNA/protein conserved binding sites provide clues that make alignment of these sequences straightforward. These landmark features are especially useful for alignment when very distantly related taxa are compared. Moreover, positions within each codon tend to evolve at different rates, with third position changes being most frequent, first position changes being highly conserved, and second position changes somewhere in between. Therefore, the reading frames in protein coding sequences provide an inherent structure useful in alignment.

Nonprotein-coding regions, such as rRNA, tRNA and other non-translated sequences are potentially more difficult to align with distantly related taxa, due in part to the lack of these landmark features. In addition, these sequences usually are

characterized by nucleotide base insertion and deletion events, presumably because there are no selective constraints to maintain reading frames that code for specific amino acids (Mindell 1991). In practice, however, the alignment of most nuclear-encoded rRNA sequences by eye does not seem to have posed significant problems because of the relatively small number of insertions/deletions and the general conservative nature of the subunits. Some regions of mitochondrial 16S rDNA may pose alignment problems in Hymenoptera because they exhibit an unusually high frequency of A's and T's relative to G's and C's (Cameron, unpublished data; Derr et al. in press). Consequently, nucleotide substitutions in these areas may be characterized by a high proportion of transversions (purine (A/G) to pyrimidine (T/C) substitutions, or the reverse) as opposed to the bias toward transitions (purine - purine or pyrimidine - pyrimidine) commonly observed in vertebrate mitochondrial genomes (Hixson and Brown 1986; Thomas and Beckenbach 1989). This becomes important when using computer alignment schemes (discussed below), which generally assign higher penalties to transversion substitutions. Also, considerable length polymorphism is evident in these AT-rich regions; large insertions and deletions (often greater than 10 base pairs in length) can further complicate alignment because of uncertain homology among the bases. It is best to exclude these hypervariable regions from the analysis. Sequences from the 16S rRNA region are depicted for three hymenopterian taxa in Fig. 3, taken from the study of Derr et al. (in press). These provide examples of insertion/deletion events, strong A/T base compositional bias, and a correspondingly high rate of transversion over transition substitutions. As a consequence of these factors, most of the

difficulties encountered in aligning nucleotide sequences involve nonprotein-coding regions.

Algorithms designed to determine the optimal alignment between two sequences have been available for some time (Needleman and Wunsch 1970; Sankoff 1972; Sellers 1974; Waterman et al. 1976). These programs attempt to maximize the number of matches or to minimize the number of substitutions, insertions, or deletions required to make two sequences equivalent (Mindell 1991). However, extending this approach to more than two sequences with no *a priori* regard to their phylogenetic relationships has been deemed inappropriate for reconstructing phylogenies (Hein 1989, 1990b; Feng and Doolittle 1987, 1990). These authors contend that in multiple alignments the initial choice of sequences for pairwise comparison can bias the final alignment, result in an excess of inferred gap events, and even affect phylogenetic results (Lake 1991). Therefore, multiple sequence alignment, at least in principle must fall under the same constraints used to infer phylogeny, in this case, global parsimony or minimizing the overall number of substitution and gap events. Alignment of sequences could be considered as part of phylogeny inference, rather than as an independent analysis (Sankoff et al. 1973). Moreover, phylogenetic congruence with other independent data sets offers a means of choosing among equally parsimonious alignments (Hillis et al. 1990).

Alignment of nucleotide sequences may be accomplished by hand and computer. Several 'progressive alignment' computer programs are currently available (e.g., Higgins and Sharp 1988; Higgins et al. 1992; Hein 1989). These programs generally proceed by: (1) calculating an initial similarity value for each pairwise comparison of sequences; (2) constructing a dendrogram by cluster analysis using the matrix of these values; and (3) aligning the sequences according to the branching order in the dendrogram. Alignment scores are calculated by assigning positive or negative values to matches and mismatches and by imposing penalties for both the insertion of gaps and for each additional change within a gap. In most cases the user may assign a numerical value for each of these penalties. Aligned sequences may then be analyzed phylogenetically using any of the currently available parsimony-based computer packages. Measures of homoplasy in the results can also be used to discriminate among various sequence alignments. In practice, results of computer alignment

procedures should always be compared with those obtained by hand, and we have found (Cameron, unpublished data; Derr et al., in press) that final computer alignments can be fine-tuned by visual inspection.

At present our understanding of the complexities of sequence comparison and analysis is still incomplete but developing rapidly. Our intent here has been to highlight the problems inherent in multiple sequence alignment as it relates to phylogenetic reconstruction, and to indicate some methods available for their solution. In general, sequence alignment is straightforward when dealing with single-copy protein-coding sequences; with non-protein coding sequences the researcher should be aware that in areas with few conserved landmark features, sequence alignment can present a number of experimental challenges. Fortunately, as the field of molecular systematics continues to evolve and as more comparative sequence data becomes available, these challenges will be met by the development of increasingly useful and realistic computer alignment algorithms. For information regarding the algorithms discussed here, refer to the work of Sellers (1974), Smith et al. (1981, 1985), Feng and Doolittle (1987, 1990). For further information on sequence alignment, homology, and weighting schemes see Mindell (1991); for general reviews see Bell and Marr (1989), Doolittle (1990), Hillis et al. (1990), Hein (1989), and Watermann et al. (1991).

Phylogenetic Analysis of Sequence Data.— Many methods have been proposed for reconstructing phylogenetic relationships with DNA sequence data for three or more taxa, and we do not propose to review them all here. Swofford and Olsen (1990) and Felsenstein (1988) provide excellent recent reviews of distance, maximum likelihood, and parsimony methods, and comment on both the logical foundations of various approaches and the 'nuts and bolts' issues of actually getting the job done. Of the various approaches currently in use, we favor a simple parsimony model for reasons of simplicity and clarity, both in analysis and in the interpretation of results. With correctly aligned sequences, parsimony analysis is relatively straightforward. Each nucleotide position is treated as an independent, unweighted character with four possible states: adenine or guanine (purines) or cytosine or thymine (pyrimidines). The simplest approach is to treat a substitution from one base to any other as equally likely ('Fitch parsimony', Fitch

1971) and this can be accommodated by treating the characters as 'unordered' or 'non-additive' (terminology differs between programs). However, because of structural constraints on the DNA molecule itself, a bias toward transitions (purine-purine or pyrimidine-pyrimidine) and against transversions (purine-pyrimidine or the reverse) has often been noted (e.g. Li et al. 1984, Hixon and Brown 1986). Some programs offer tools to accommodate differential weighting of some character state changes over others. For example, the 'Step Matrix' function in PAUP (Swofford, 1990) can be used to assign any integer weight for changes between any two character states. Of course, the problem is to determine what weights to assign. In highly AT-rich sequences such as are found in many Hymenoptera, many changes necessarily will be from A to T or the reverse (transversions), and there may not be a bias towards transitions. It is possible, at least in theory, to examine empirically the base composition of sequences and to derive from these the expected probabilities for the different categories of substitution. Swofford and Olsen (1990) make a sensible suggestion: by giving only slightly lower weight to transversions, the weights will come into play only in choosing between essentially equally parsimonious solutions, and transitions will then be given the edge.

A strategy to reduce the effects of homoplasy with sequence data from protein-coding genes is to eliminate nucleotides in the third position of each codon, or to give them a lower weight. This is based on the redundancy of the DNA code; that is, in most cases the first two positions of the code are sufficient to specify an amino acid and the third may be redundant information. As a result, substitutions in third positions may accumulate more rapidly than in the other positions. If more than one substitution has taken place, the position is no longer informative. Although this approach is usually limited to protein-coding genes, in an analogous fashion, if the secondary structure of non-protein-coding sequences is known, regions shown to be undergoing compensating substitutions can be eliminated (Wheeler and Honeycutt 1988), or preferably, given an appropriate lower weight (Vawter, 1991).

For analysis of small data sets, any up to date computer algorithm for parsimony analysis will suffice but we recommend using a recent version of one of the readily available algorithms such as PAUP (Swofford 1990) or Hennig86 (Farris 1988).

For studies with fewer than 15-20 terminal taxa, one of the exact methods can be used (branch and bound, exhaustive search, or implicit enumeration), and one can be confident that the most parsimonious tree or trees have been found. For larger datasets or those with relatively high levels of homoplasy, heuristic search procedures such as branch-swapping will be required. In such cases, it is important to try many different addition sequences and search procedures, until one's patience has literally been exhausted, because it is often difficult to escape local optima in which the algorithms become trapped, or to find all of the different groups (or 'islands') of equally parsimonious solutions (Maddison 1991).

A problem that is more or less unique to sequence data is how to handle insertion and deletion events, for example, as inferred by alignment procedures. A conservative approach is to treat gaps in sequences as missing data. In this case they will have no effect on tree length or character state optimization. However, insertions and deletions may represent real phylogenetic events and this approach ignores their potential contribution to phylogenetic reconstruction. An alternative is to treat insertions and deletions as separate characters, but if they vary in length, one will encounter problems in establishing their homology and the transformation series among them. One's choice of approach should be governed directly by the data.

Outgroup Selection.— Outgroups may be used to determine character polarity or to root unrooted trees following a parsimony analysis (Watrous and Wheeler 1981; Donoghue and Cantino 1984; Maddison, Donoghue, and Maddison 1984). For Hymenoptera, selection of an outgroup for taxa at the rank of subfamily or above is often problematical. For example, although the Symphyta are perhaps best thought of as a basal paraphyletic group within the Hymenoptera, there are several competing hypotheses of relationships among symphytan groups (Ross 1937; Königsman 1977; Rasnitsyn 1980, 1988; Gibson and Goulet 1988). These alternative hypotheses affect both the choice of an outgroup for the remaining Hymenoptera (the Apocrita) as well as hypotheses of character state evolution within various symphytan lineages. Within the Apocrita, relationships among the non-aculeates are particularly problematical. Recent suggestions (Rasnitsyn 1988; Mason, unpublished data) that the Aculeata are the sister group to the Ichneumonidea would have a significant impact

on character polarities within those groups, but this hypothesis remains relatively untested. Similar problems are apparent for larger groups throughout the order. Indeed, at the ordinal level, there is virtually no agreement on the appropriate sister group to the Hymenoptera as a whole. Until higher level relationships among the Insecta are better known, the choice of an appropriate outgroup will continue to be a problem for studies of phylogenetic analyses within Hymenoptera, regardless of the type of evidence used.

Why might the choice of outgroup be critical when using molecular data for phylogeny? Wheeler (1990) has recently discussed some of the problems posed by distant or uncertain outgroups when using molecular data. If distantly related taxa are used as outgroups, the probability that sequence similarity is due to random identity increases, and the chance that any one character is phylogenetically informative consequently decreases. If outgroup taxa are sufficiently divergent, polarization of characters essentially becomes random. In essence, results become phenetic, rather than phylogenetic.

How can this affect results of parsimony analyses? If sequences are too divergent, an ingroup may not be resolved as monophyletic relative to multiple outgroups. We encountered this problem when using two Diptera, *Aedes* and *Drosophila*, as outgroups to Hymenoptera (Derr et al., in press). The two dipterans were nearly as divergent from each other as they were from some of the Hymenoptera, resulting in instability at the base of the tree. In fact, in this case Hymenoptera could not be resolved as monophyletic relative to Diptera, clearly an unsatisfactory result.

Assessing the Reliability of Results.— Bootstrap methods in combination with parsimony procedures have become popular in recent years as a way to assess the degree of support for a particular phylogenetic clade (Felsenstein 1985, 1988). Bootstrapping involves random sampling with replacement from a set of characters until a new character set is formed, equal in number to the original set. From this new character set, another maximum parsimony tree is estimated. The procedure is repeated many times (e.g. 100–10,000) and a distribution of solutions is obtained. Several assumptions underly bootstrap analysis (Felsenstein 1985, 1988). One is that nucleotides evolve entirely independently of one another, that DNA initially consists of unlinked sequences of nucleotides that change at random throughout the molecule. An-

other is that nucleotides are identically distributed for all taxa. The first assumption may be violated with hymenopteran mtDNA. Our investigations (discussed below) indicate that hymenopteran mtDNA is highly AT-rich and that A-T transversions are far more likely than other types of transversional substitutions. This is a clear violation of the equal probability assumption, which predicts that only 1/4 of all transversions should be A-T transversions. Another violation of the independence assumption arises with sequence data if secondary structural constraints in the molecule result in compensating substitutions (Wheeler and Honeycutt 1988; Simon et al. 1990), such as Vawter (1991) found for a relatively small number of bases in the stem region of insect rRNA. However, with bootstrap one can take these biases into account (just as with parsimony analysis) by applying, for example, less weight to A-T transversions or to sequences with known compensating substitutions. The second assumption, that characters are identically distributed, poses a difficulty if sequences are selected from different regions of the genome with different distributions. Also, mixing morphological and molecular data in a single bootstrap analysis would violate this assumption if the two character sets reflect different distributions (e.g., continuous and discrete; normal and Poisson). Bootstrap percentages are often interpreted as confidence intervals associated with particular topologies. However, this is appropriate only for testing the validity of a single lineage that has been identified in advance of the analysis (Swofford and Olsen 1990) and if the above assumptions are met. Violation of these assumptions severely reduces the accuracy of the reported confidence intervals (Sanderson, 1989). Even though the assumptions of the bootstrap may be restrictive, it is nonetheless a valuable heuristic method for testing the robustness of results from parsimony analyses. For example, the appearance of a particular group or clade in all or most (e.g. 85–95%) of the replicates may be used as an index of support for its monophyly (Swofford and Olsen 1990).

One may also wish to know whether a given set of characters support one tree topology significantly more strongly than another topology under the assumption of parsimony. Templeton's paired comparisons test compares two trees in this fashion. This test is an application of Wilcoxon's non-parametric signed-ranks test, using Templeton's criteria for nucleotide sequence data (Templeton

1983). The scoring procedure involves counting the number of substitutions at each informative site for two given trees and applying the Wilcoxon test to the hypothesis that the total number of substitutions is equal for the two trees. Also, additional information can be incorporated into the scoring procedure. If, for example, it is known that transversions are more common than transitions in a given region of DNA, one might choose to give more weight to transitions by assigning them a higher score than transversions (e.g., transitions = 2, transversions = 1). Templeton's test is conservative, thus it is difficult to reject the null hypothesis without large differences in the number of substitutions between the two trees. This is one of the strengths of the procedure.

Felsenstein has developed a test that uses similar data to investigate relationships among sets of three taxa, following the statistical approach of Cavender (1981). Cavender pioneered methods for applying confidence intervals to phylogenies based on parsimony, and Felsenstein (1985) later modified Cavender's methods to include sequence data. For a group of three taxa (rooted with an outgroup), there are three possible alternative tree topologies. Two statistics are used to evaluate whether the most parsimonious topology is significantly better than the other two at the 95% confidence level: *S* is the number of additional steps that a tree must have to be significantly worse than the most parsimonious tree; *C* is the number of phylogenetically informative characters that must support a tree topology for it to be significantly better than the others (Felsenstein 1985). Like Templeton's test, this test is conservative; a tree topology that differs by only a few steps, or is supported by only a few more characters will not be significantly different. Felsenstein's test assumes a molecular clock (i.e., that the number of changes in a lineage is roughly proportional to the amount of time since its divergence), a controversial assumption which has only just begun to be examined in insects (Crozier et al. 1989).

One final caveat: if data are homoplastic, multiple models of character state change may be possible on a given minimum-length tree topology. The simplest example is a case in which a parallelism or a reversal is equally parsimonious, and either may be used to explain the data. Parsimony programs contain a number of tools, known as 'optimization' methods, to assist in modeling character state change on cladograms. We caution against

the use of any one criterion, for example, minimizing parallelisms or reversals. In principle, the best approach is to determine all of the possible alternative models of character state change for each equally parsimonious tree topology. In practice, this is feasible only if relatively few characters are involved; with sequence data the alternatives are likely to be numerous and complex. A workable alternative is the use of tree diagnostics, which show the minimum and maximum number of steps possible in each interval on the tree under all possible models of character state change.

EXAMPLES OF CURRENT RESEARCH

Tribal Phylogeny of the Family Apidae.—The focus of this investigation was to examine the usefulness of DNA sequence data for resolving phylogenetic relationships among tribes of the family Apidae. Sequences from the mitochondrial 16S rRNA gene were compared in 15 exemplars representing the four apid tribes (Cameron, 1991). The exemplar approach was justified on the basis that the tribes (considered as subfamilies by Michener 1990) have been recognized as monophyletic groups. The use of several taxa (as many as is practicable for the study) to represent each clade is important for several reasons. First, the use of multiple taxa will help to resolve the degree of sequence variation exhibited within a given region (e.g., variation among species within a tribe or variation among tribes), hence assist in the selection of regions appropriate for a given level of inference. Second, using multiple exemplars from each clade should help to eliminate random error or potential biases that could affect the evaluation of alternative phylogenies. At least two individuals of each species were sequenced as a check against sequencing errors and potential intra-specific variation. Sequences were obtained from fresh, frozen, and ethanol-preserved tissue. The outgroups for the analysis were selected from the subfamily Xylocopinae (family Anthophoridae), considered to be monophyletic and the closest relatives of Apidae (Sakagami and Michener 1987). Two outgroups were selected from two different xylocopine tribes (Xylocopini and Allodapini).

Between 500 and 600 bp were sequenced from the 3' end of the 16S rRNA for all 17 taxa. Sequencing was accomplished using two primers (Fig. 4; Appendix 1) designed to optimize the match between published sequences from the 16S mitochondrial

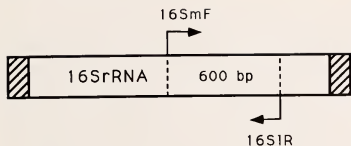


Fig. 4. A representation of the mitochondrial 16S (large subunit) rRNA gene, flanked by transfer RNAs (hatching). The two outside arrows correspond to the position and direction of extension of the oligonucleotide primers used in PCR and sequencing reactions (Cameron, 1991, unpublished data). Dotted lines circumscribe the approximate 600 bp region of the gene that was amplified with PCR.

rRNA of the honey bee *Apis mellifera* L. (Vlasak et al. 1987) and partial sequences obtained for other apid taxa with the use of 'universal' primers (Kocher et al. 1989; John Patton, unpublished data). From the total number of nucleotides sequenced, 116 were informative in the sense that at least two ingroup taxa shared substitutions at those sites. A gap was considered as a fifth character, which did not give undue weight to deletions as gaps were rare among the informative sites. Length polymorphisms were evident in the 16S rRNA of every taxon, but these were not included as characters. Transition and transversion substitutions were treated with equal weight in the analysis. The sequences were aligned by hand and checked by computer alignment using the Treealign Computer Program (Hein 1990a). The issues of length polymorphisms, character weighting, and alignment are treated in detail above (see Phylogenetic Analysis of Sequence Data).

The 116 informative sites from the 15 ingroup taxa and one of the outgroups, *Xylocopa virginica* (L.), were analyzed using maximum parsimony techniques implemented in PAUP (Version 3.0L, Swofford 1990). Maximum likelihood (Felsenstein 1981) and bootstrap analyses (Felsenstein 1985) were implemented as heuristic methods to test for the reliability of the results based on maximum parsimony. Two equally parsimonious trees were produced (Figs 5A, 5B). In tree A, Apini + Euglossini comprise one clade and Bombini + Meliponini comprise a second clade. In tree B, the Bombini + Meliponini clade is retained, with Euglossini as its sister group. The results are consistent with monophyly of each of the currently recognized tribes, except Bombini, which appears to be paraphyletic with respect to Meliponini (trees in-

dicating the monophyly of Bombini were only two steps longer). Both bootstrap and maximum likelihood analyses strongly supported the Bombini + Meliponini clade. To test for effects of the choice of outgroup, an additional outgroup (Allocladini: *Exoneura*) was included in a separate analysis. This resulted in two maximum parsimony trees, each with the same tribal topology as tree A (Fig. 5). Future work should include additional analyses of more distantly related outgroup taxa from the Anthophoridae.

The sequence information obtained from the 16S region had some interesting characteristics, including a higher proportion (> 80%) of A and T bases and a correspondingly high number of transversion-substitutions. Length polymorphisms almost exclusively comprised strings of A's and T's. The occurrence of large insertions and deletions resulted in the exclusion of sections of the sequences from the analysis because of questionable alignment. Nonetheless, this region was sufficiently conserved overall to be useful for resolving relationships at the tribal level. The instability of the apini branch can probably be resolved by including sequence information from additional representatives of the Euglossini. Because of space considerations, the aligned sequences and information regarding percent sequence divergence,

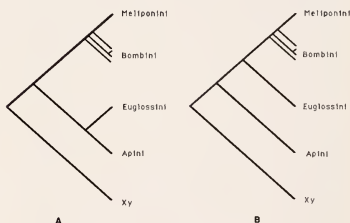


Fig. 5. The two most parsimonious trees (A and B) for the tribes of Apidae, inferred using the branch and bound method implemented in PAUP (from comparisons of nucleotide sequences of mtDNA [16S rRNA] from 16 taxa). The trees are simplified to show only the tribal topology. The outgroup is *Xylocopa virginica* (Anthophoridae). Tree length for analyses of 116 informative sites in 16 taxa was 304 steps, resulting in a consistency index of 0.533.

base composition, and base distribution have been omitted and will be presented elsewhere (Cameron, unpublished data).

Species Phylogeny for the Genus *Apis*.—The same sequences from the 16S mitochondrial rRNA subunit (500–600 bp) discussed above were used in a separate analysis of five species of the genus *Apis*. These included *A. mellifera*, *A. cerana* F., *A. koschevnikovi* Buttel-Reepen, *A. dorsata* F., and *A. florea* F. One or more exemplars were selected from each of the three remaining apid tribes (Meliponini, Bombini s.s., and Euglossini) and Xylocopinae (*X. virginica*) to serve as outgroups. This study represents a case in which comparative sequences for a given region are useful for two different levels of analysis. From the original data set (above) there were 36 informative sites within *Apis*. Maximum parsimony trees, based only on the informative sites, were estimated in separate analyses using each of the outgroups. Two equally parsimonious ingroup trees were produced: (Figs 6A, 6B). Tree A is concordant with recent analyses based on morphology (Alexander 1991) and comparative sequences from the mitochondrial subunit II of the cytochrome-oxidase gene (COII) (Garner et al. 1991). A well-corroborated pattern of this nature, utilizing three independent data sets, is highly desirable for two reasons: (1) it suggests a high level of reliability in the phylogenetic pattern, and (2) offers strong support for the acceptance of hypothesis A over hypothesis B (Fig. 6). A complete discussion of these results will appear elsewhere.

Relationships Among the Higher Levels of Hymenoptera: mtDNA.—The focus of this study was to examine the phylogenetic utility and the degree of resolution provided for various hierarchical levels within Hymenoptera by nucleotide sequence information from the 16S rRNA region of the mitochondrial genome (Derr et al., in press). Representative DNA sequences from two members of the suborder Symphyta (superfamilies Siricoidea and Tenthredinoidea) and seven from the suborder Apocrita (superfamilies Ichneumonoidea, Chalcidoidea and Vespoidea) were examined and compared. In addition, published 16S rRNA sequences from *Aedes* (HsuChen et al. 1984) and *Apis* (Vlasak et al. 1987) were included in the analysis. Multiple individuals and clones were sequenced from each taxon. We were able to obtain usable sequences from specimens killed and preserved in 70% ethanol. Sequences from smaller species (*Aphytis*, Aphelinidae) were obtained from pro-

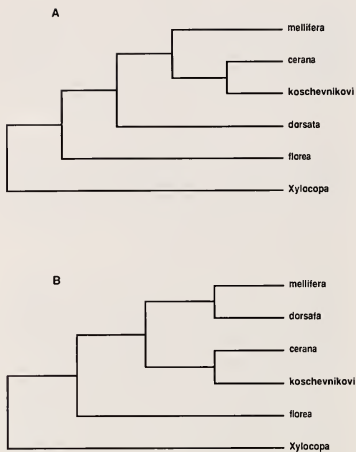


Fig. 6. The two most parsimonious trees (A and B) for *Apis*, inferred using the exhaustive search method implemented in PAUP from comparisons of nucleotide sequences of mtDNA (16S rRNA) from 6 taxa. The outgroup is *Xylocopa virginica*. Tree length for analyses of 6 taxa was 118 steps for 36 informative sites, resulting in a consistency index of 0.643.

geny of single females (isolines). Details regarding DNA isolation, PCR, cloning and sequencing will be provided elsewhere (Derr et al. in press).

Following computer-assisted alignment of the sequences, a total of 573 nucleotide positions was reported with 287 variable in two or more taxa. Each of these sequences was characterized by numerous insertion/deletion events and a bias for A and T bases (cf. Fig. 3). Percent A and T ranged from 0.533 to 0.794, with sequences from members of Ichneumonoidea and Chalcidoidea displaying significantly lower A and T averages. Moreover, sequences from both of these superfamilies also exhibited significantly more strand asymmetry, with an unequal number of purines (A and G) or pyrimidines (T and C) on each DNA strand.

Pairwise comparison among all taxa revealed percent sequence differences ranging from a low of < 2.5% to a high of slightly over 50%. These se-

quences were analyzed using maximum parsimony and bootstrap procedures available in PAUP (Swofford 1990). This analysis, which included rooting with 16s rRNA sequence from the dipteran *Aedes*, resulted in a single most parsimonious tree (Derr et al. in press). A bootstrap consensus tree derived from 100 replications had an identical topology. Two major groups of hymenopteran taxa emerged; the first included the symphytans and the aculeates, the second comprised the parasitic Hymenoptera. However, examination of less parsimonious trees revealed another solution only two steps longer (out of 703 total steps) in which the Symphyta form a basal grade to a monophyletic apocritan clade (aculeates plus parasitic Hymenoptera). All internodes were well supported in the bootstrap analysis with the notable exception of those leading to the Symphyta and the aculeates.

An additional analysis, using one of the two symphytans as an outgroup to the apocritan taxa, also resulted in a sister group relationship between the aculeates and the parasitics. This confirmed the instability at the base of the tree and suggested that a high level of sequence divergence precludes using this region for resolving relationships at the subordinal level. Nevertheless, these results support both the aculeates and at least these parasitic Hymenoptera as distinct monophyletic groups, and provided baseline information regarding the amount and type of nucleotide sequence information available from this region. Interestingly, the sister group relationship between Ichneumonoidea and Chalcidoidea is probably the most strongly supported result to emerge from the analysis. Among the parasitics, the three representatives of the Ichneumonoidea form a monophyletic group. However, sequence divergence among the ichneumonoids was low, providing little resolution among the terminal taxa. Conversely, the two chalcidoid sequences examined, both from the genus *Aphytis*, clearly represented a monophyletic group and they are very divergent from one another, suggesting that this region may have considerable utility at the species level. Baseline information of this type allows subsequent investigations to focus on areas of the genome most likely to produce phylogenetically useful information.

Relationships Among the Higher Levels of Hymenoptera: Nuclear rRNA.—An exploratory study to examine the usefulness of partial sequences of the small-subunit rRNA for higher-level phylogenetic applications within the Hymenoptera has recently been completed (Austin et al. unpublished

data). Although the final results of our investigation are not yet available (and will be published elsewhere), some points can be made that should prove useful to workers who are interested in the molecular systematics of Hymenoptera.

We wished to examine three hypotheses: the paraphyly of the Symphyta, the basal position of the Stephanidae to the rest of the Apocrita, and the sister-group relationship between the Ichneumonoidea and Aculeata (see Whitfield this issue for more information and references to these hypotheses). Initial trials were made with five divergent taxa (*A. mellifera*, *Perga dorsalis* Leach, *Sirex noctilio* F., *Megarhyssa nortoni* (Cresson) and *Ibalia leucospoides* Hochenwarth). Multiple species from some of these five lineages were examined to check the reliability of these data and to test the various methods of analysis against confirmed monophyletic groups. Overall for the ingroup, we collected sequence information from three ichneumonoids (two ichneumonids and a braconid), two pergid sawflies and two aculeates (*A. mellifera* and *Myrmecia* sp.). Because the sister group to the Hymenoptera is unknown, we employed multiple outgroups: *Drosophila*, *Artemia* (published sequences, Dams et al. 1988), and two species of water beetle (newly sequenced as part of another study).

Results obtained using three commercially available universal primers for the 18S subunit rRNA (A, B and C, Field et al. 1988; Baverstock et al. 1991a) revealed a mean sequence divergence of about 5% among the taxa. Two other primers (D and E, Baverstock et al. 1991a, 1991b), reportedly specific to more variable regions of the 18S subunit (Baverstock et al. 1991b), yielded sequences with 3.3% to 17% divergence. These regions proved too conservative to test the above hypotheses. Additional sequence information collected from six other species basically confirms the high degree of conservation within the small-subunit ribosomal RNA, a result which is consistent with those of Sheppard and McPheron (1991) for the Apidae.

It is our opinion that sequences from the large-subunit (28S) rRNA, which have been useful in a preliminary investigation of higher level relationships (Sheppard and McPheron 1991), combined with mtDNA and nuclear DNA sequences obtained with PCR technology, will be most fruitful for examining hypotheses of relationships among suborders and families of the Hymenoptera.

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APPENDIX 1. MITOCHONDRIAL DNA PRIMERS

The following primers are based on hymenopteran mtDNA sequences and have been successfully employed on a range of species (Cameron 1991; Cameron unpublished data). All primers are written in the 5' to 3' direction. Primers are named for the gene in which they are located (e.g. 16S), their relative position in the gene (m=mid, l=low), and whether they prime in the forward (F) or reverse (R) direction. Two nucleotides at a single position (one below the other) represent a degenerate site (a nucleotide site occupied by more than one nucleotide). Degeneracy in the primer allows for some degree of mismatch between the primer and its complementary target.

16S rRNA Primers

875-16SmF (24mer)	
<i>Apis</i>	5'-TTATTACACGTGTTTATCAAAACAT-3'
874-16SlR (20mer)	
<i>Apis</i>	5'-TATAGATAGAAACCAATCTG-3'
	C
16SmR (20mer)	
<i>Cotesia</i>	5'-CAGGTGAATATAAATTTGCC-3'
(Braconidae)	

12S rRNA Primers

12SmF (20mer)	
<i>Bombus</i>	5'-CTTATTAGAGAACTGTAG-3'

Genetic Relatedness and Population Structure in Primitively Eusocial Wasps in the Genus *Mischocyttarus* (Hymenoptera: Vespidae)

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Abstract.— Protein electrophoresis was used to investigate the genetic structure of two species of *Mischocyttarus*, a genus of primitively eusocial wasps. To do this we develop methods for estimating relatedness when there is population structure above the level of the colony. Relatedness among female colony-mates was quite high, consistent with the observations that only one or a few females had developed ovaries. One species, *M. basimacula*, showed no population structure above the colony level. The other, *M. immarginatus*, had a high inbreeding coefficient, which seems to arise from genetic differentiation of subpopulations that are less than 400 m apart. This subdivision means that individuals are quite closely related even to members of their own subpopulation who are not colony-mates. We discuss the possible relevance of these results to the evolution of the multiple-queen epiponine wasps.

The polistine wasp genus *Mischocyttarus* occupies a special position for the study of the evolution of sociality in the Vespidae. It includes approximately 200 species, most of them in the neotropics but a few extending into Western North America and Florida (Richards 1978). *Mischocyttarus* is classified as primitively eusocial; although most individuals function as workers, there are no morphologically specialized castes. Since worker behavior is not pre-determined by morphology, primitively eusocial groups are especially suitable for studies of the selective advantage of worker behavior. Behavioral studies (Jeanne 1972; Litte 1977, 1979, 1981; Rodriguez 1989) have shown *Mischocyttarus* to be similar to the better-known genus *Polistes* in having a single queen who gains egg laying privileges by behaviorally dominating other females, although Itô (1984) has noted some tendency towards polygyny. However, *Mischocyttarus* is more interesting than *Polistes* in one respect, its phylogenetic position. It is more closely related (possibly the sister group) to an interesting and successful taxon of neo-tropical social wasps known as the Epiponini (Carpenter 1991, in press). The Epiponini are a clade of some 200 species that are socially more complex in several respects: (1) new colonies are founded by swarms of queens and workers, (2) colonies typically have multiple queens, and (3) castes are morphologically differentiated in some species (Richards 1978; Jeanne 1980, 1991). Since *Mischocyttarus* is closely related,

and possibly the sister group, studies of this genus might yield insights into the evolutionary history behind the traits that characterize the epiponines.

In this paper we focus on the genetic structure of two species of *Mischocyttarus* from the Yucatán peninsula of Mexico, *M. immarginatus* (Richards) and *M. basimacula* (Cameron). Hamilton (1964a, 1964b) showed that reproductively altruistic behavior such as that shown by social insect workers is promoted by high relatedness; genes for altruism will be lost unless the altruists aid individuals who share those genes. High relatedness is especially important in primitively eusocial species because workers are more likely to have the option of reproducing by themselves. Studies of primitively eusocial insects have generally confirmed this expectation (Metcalf and Whitt 1977; Lester and Selander 1981; Crozier et al. 1987; Schwarz 1987, 1988; Kukuk 1989; Ross and Matthews 1989; Strassmann et al. 1989). However, relatedness is usually lower within colonies of swarm-founding epiponines (Queller et al. 1988; West-Eberhard 1990; Strassmann et al. 1991) presumably because they often have several or many queens with developed eggs (Richards 1978; Jeanne 1980, 1991). It therefore seems possible that the same is true in their possible sister group, *Mischocyttarus*, particularly given Itô's (1984) finding (in two species, including *M. basimacula*) of multiple egg-laying females in the same colony. We have previously reported average relatedness among female colony-mates for *M.*

immarginatus and *M. basimacula* and found it to be high (Strassmann et al. 1989), which seems inconsistent with them having many queens.

Even if *Mischocyttarus* does not have multiple queens, it is still possible that it holds a different kind of key to understanding the evolution of multiple queens in its sister group. The relatedness-lowering effect of multiple queens might best be tolerated in social species that previously had very high relatedness. Inbreeding and population viscosity have been suggested as two population characteristics that might raise relatedness in this context (Hamilton 1972). If either of them operates in *Mischocyttarus*, then it may have also operated in the putative common ancestor of *Mischocyttarus* and the epiponines. In this report we focus on the effect of population structure above the colony level on genetic relatedness.

METHODS

Colonies, defined as a comb along with its resident adults, were collected in December 1987 during the dry season in Yucatán, México. Colonies of both species were located on buildings, usually on the underside of thatch eaves or in gaps within the thatch. Nineteen colonies of *Mischocyttarus immarginatus* were collected from three clusters located within 400 m of each other near the Uxmal archeological site. Three colonies of *M. basimacula* were collected from this site and 13 additional colonies were collected from 3 similarly close clusters near the Chichén Itzá archeological site, 130 km away. In both species, colonies within each cluster were no farther than 20 m from all other colonies in the cluster. All colonies within each cluster were collected, except as noted below, and we found no additional clusters in the areas between the collected ones. Our analyses will sometimes use these clusters of colonies as an additional level (which we will call the subpopulation level) at which interesting genetic structuring might occur. The clusters were not centered on colonies of more aggressive wasps, as has been reported for *M. immarginatus* (Windsor 1972).

Because some colonies were awkwardly positioned between layers of thatch, we were not always able to capture all of the adults. When any adults escaped, care was taken to see that they did not alight on neighboring nests. They did sometimes return to nearby abandoned nests, but did not generally alight on occupied nests before we could

collect them. On one or two occasions when this was uncertain, we did not collect the neighboring nest that might have been contaminated by foreign wasps.

The adults we captured were kept alive on ice for several days until they could be transferred to a low temperature (-70°C) freezer. Nests were scored for contents, stored on ice for several days, and then were kept in separate enclosures to allow pupae to emerge as adults. The 23 *M. immarginatus* females that emerged were deep frozen with the other adults and were later included in our analyses. The single female of *M. basimacula* that emerged was discarded.

The frozen adults were retrieved, dissected to determine ovarian condition, and subjected to protein electrophoresis. Standard starch gel methods, described in detail elsewhere (Strassmann et al. 1991) revealed three useful polymorphisms in *M. immarginatus* and two in *M. basimacula*. Males were scored as an aid in characterizing the Mendelian nature of the polymorphisms. However males were not included in the statistical analyses because they were few in number.

Relatedness estimates were obtained using the general method of Queller and Goodnight (1989). Below we extend the technique to fit populations that may be structured at the colony level and also at a higher subpopulations level. A brief description of the method is necessary to set the stage for extending it to sub-divided populations. For relatedness of one set of individuals, x , to another set, y , the basic estimator can be written as follows:

$$\frac{\sum_i \sum_k \sum_a w(p_{im} - p_m^*)}{\sum_i \sum_k \sum_a w(p_{im} - p_m)}$$

This is formula 10 of Queller and Goodnight (1989), with notation slightly altered. Summations are over all individuals of interest (i), loci scored in that individual (k), and the two (for diploids) allelic positions at that locus (a). The p_m 's are various frequencies of the allelomorph currently being summed over (the one at position a of locus k of individual i); p_{im} is the frequency of that allele in individual i itself; p_m is the frequency of the set of i 's relatives whose relatedness is being estimated; and p_m^* is the frequency of the allele in the base population. The w is a statistical weight which can be chosen to give greater weight to certain individuals or to certain loci. This formula estimates the

relatedness coefficient proposed by Grafen (1985) and it is easy to see why it is a good descriptor of how selection works on behaviors that affect both an altruist and its colony members. The numerator totals up identities of potential altruist genes with genes of other colony members, and then subtracts the identities expected by chance, leaving an estimate of identity by descent. In the same way, the denominator estimates identities by descent of altruist's genes with their own genotypes. The ratio therefore describes the relative value of the altruist and of other colony members as vehicles for the propagation of the altruist's genes.

The asterisk of p_m^* serves to indicate a correction necessary to remove a bias present in earlier relatedness measures (Pamilo and Crozier 1982; Pamilo 1984, 1989). To get an unbiased estimate of the differences in the numerator and the denominator, it is necessary that the first and second terms of these differences be estimated independently (Queller and Goodnight 1989). How this is accomplished is best illustrated by example. Suppose we have a population subdivided into colonies, indexed by values of c , and we want to estimate average relatedness to colony mates. Formula 1 can be written as:

$$r = \frac{\sum_i \sum_k \sum_a w(p_{c(i)m} - p_{c(k)m})}{\sum_i \sum_k \sum_a w(p_{im} - p_{c(k)m})}$$

Here the set of relatives of interest is all colony mates except for the individual itself, so the frequency of allelomorph m in these relatives is written as $p_{c(i)m}$. The population frequency of this allele, estimated to avoid bias, is written as $p_{c(i)m}^*$, that is, the population frequency is estimated after excluding the current colony. This means that the estimate of the population frequency changes slightly according to which colony the potential altruist belongs to. This step is necessary whenever we have a small sample of colonies drawn from a much larger population. Including the colony in the estimate would lead to an overestimation of its contribution to the population frequency and therefore an underestimation of the difference from the colony frequency.

When there is population structure above the level of the colony (sub-populations or demes), then several different r 's may be of interest. Pamilo (1984, 1989) gave these names analogous to F-statistics.

The relatedness to colony mates with respect to the total population is called r_{ct} . This is essentially the measure described above, although it should be estimated slightly differently when there is sub-population structure (see below). Relatedness to members of the whole sub-population (other than one's own colony) is called r_{st} . It would be relevant to describing selection on a broader kind of altruism that extends beyond the confines of the colony to the whole sub-population. Finally r_{cs} is the relatedness of colony members with respect to their own sub-population rather than with respect to the whole population. This relatedness is the one that is most relevant to the spread of colony altruism alleles within isolated sub-populations that are evolving relatively independently.

Table 1. Estimation of relatedness. Table entries are the frequencies of allelomorph m required for using equation 1 to estimate various measures of relatedness. The first r is for estimation under the assumption of no population subdivision above the colony level. The others estimate relatedness within colonies with respect to the total population, within colonies with respect to their own subpopulation, and within subpopulations with respect to the total population.

relatedness measure	frequency in relatives (p_{im})	frequency in population (p_m^*)
r	$p_{c(i)m}$	$p_{c(i)m}$
r_{ct}	$p_{c(i)m}$	$p_{c(i)m}$
r_{cs}	$p_{c(i)m}$	$p_{st-c(i)m}$
r_{st}	$p_{st-c(i)m}$	$p_{c(i)m}$

Estimates for these three relatedness parameters are obtained using formula 1, with the substitutions indicated in Table 1. The estimate for r_{ct} is the same as that for r without population structure (formula 2) except that the estimate of population frequency necessary to avoid bias is slightly different. Now, this frequency should be calculated excluding the whole sub-population ($p_{c(i)m}$) instead of just the colony. The same procedure is required for r_{st} . The corresponding measure for r_{cs} is the frequency in the sub-population, after having excluded the current colony ($p_{st-c(i)m}$). The only change is that for r_{st} , the set of relatives of interest is the subpopulation (except members of the individual's

own colony).

These statistics can be related to each other by a formula analogous to one well-known for F-statistics: $1 - r_{st} = (1 - r_{ca})(1 - r_{st})$ (Pamilo 1984). The estimators of these statistics developed here also possess this property.

F-statistics are estimated in analogous fashion (Queller and Goodnight 1989, equations 13-15). In the absence of sub-population structure, the inbreeding coefficient can be estimated as

$$f = \frac{\sum_i \sum_k \sum_a w(p_{i(a)m} - p_{(-)cm})}{\sum_i \sum_k \sum_a w(1 - p_{(-)cm})}$$

where $p_{i(-)cm}$ is the frequency of allelomorph m in the individual i , i , currently being summed over, but not including the allelic position, a , currently being summed over. In other words, it is the frequency at the other allelic position. Other than changes in notation, this differs from the estimate for F_{st} (Queller and Goodnight 1989, equation 14) only by using $p_{(-)cm}$ instead of $p_{(-)cm}$ as the estimate of the population frequency. This is exactly analogous to the already-noted difference between r and r_{st} .

For all estimates in this report we weight colonies equally, so w is set equal to the reciprocal of the number of females scored. To obtain standard errors for most estimates, we jackknife (Sokal and Rohlf 1981) over colonies, which simulations show to be a satisfactory procedure (Queller and Goodnight 1989). The exceptions are the sub-population parameters, r_{st} and F_{st} , which are jackknifed over sub-populations (because there are few sub-populations, these estimates are less reliable). For both relatedness and F-statistics, the jackknife standard errors can be used to construct confidence intervals or to conduct t-tests using t distributions with degrees of freedom equal to one less than the number of colonies (or sub-populations for r_{st} and F_{st}) (Sokal and Rohlf 1981).

RESULTS

Table 2 shows characteristics of the colonies of both species. Both were raising brood during the dry season, although some colonies, especially of *M. basimaculata*, had little or no brood. On average, *M. basimaculata* colonies were raising fewer brood than *M. immarginatus*, as can be seen most clearly from the difference in the percent of cells containing pupae or large larvae. In each species there were some new nests, identified by the absence of

Table 2. Colony characteristics of *Mischocyttarus* species (means \pm standard deviations).

	<i>M. basimaculata</i>	<i>M. immarginatus</i>
cells	61.5 \pm 42.1	54.5 \pm 51.8
pupae	4.2 \pm 3.6	9.3 \pm 9.7
large larvae	2.8 \pm 2.6	5.9 \pm 5.2
(pupae + large larvae) / cells	0.17 \pm 0.12	0.33 \pm 0.16
adults with layable eggs *	2.44 \pm 1.96	2.18 \pm 2.37

*Since some adults escaped capture, this is an underestimate.

pupae and of cells bearing the remnants of pupal cocoons.

In each species the arithmetic mean number of females with layable eggs per colony exceeded two (Table 2). The modal number was one. If all the females with layable eggs are actually successful at laying them and having them raised, then this should tend to lower relatedness within colonies. However, Wade (1985) has shown that the correct measure for considerations of the effect of queen number on average relatedness is the harmonic mean number of egg layers (this is because relatedness is a function of the reciprocal of queen number, and the harmonic mean involves the mean of reciprocals). The harmonic mean number of egg layers is 1.54 for *M. basimaculata* and 1.27 for *M. immarginatus* (for this measure, colonies in which no disseeded females had layable eggs were assigned as having one egg-layer). It should be remembered that these numbers are probably slightly lower than the actual numbers since some females escaped capture.

Tables 3 and 4 list the allele frequencies for the polymorphic loci. The estimates of relatedness and inbreeding, assuming no population structure above the level of the colony, are given in Table 5. Female colony mates in both species are highly related, with the value for *M. immarginatus* being particularly high and very close to that expected for the progeny of one singly-mated outbred female (0.75). However, *M. immarginatus* does not fit this model because it is highly inbred. There is no evidence for inbreeding in *M. basimaculata*.

Estimates of F-statistics, reported in Table 6, can reveal some additional aspects of population struc-

Table 3. Allele frequencies in *Mischocyttarus basimacula*. GPI = glucose-phosphate isomerase; PEP = peptidase. All frequencies are calculated by giving each colony equal weight.

	# colonies	# individuals	GPI		PEP	
			a	b	a	b
whole population	16	75	0.57	0.43	0.98	0.02
subpopulation 1	3	24	0.57	0.43	1.00	0.00
subpopulation 2	5	21	0.58	0.42	0.96	0.04
subpopulation 3	5	21	0.60	0.40	0.97	0.03
subpopulation 4	3	9	0.51	0.49	1.00	0.00

Table 4. Allele frequencies in *Mischocyttarus immarginatus*. PGD = 6-phosphogluconate dehydrogenase; PGM = phosphoglucomutase; GDA = guanine deaminase. All frequencies are calculated by giving each colony equal weight.

	# colonies	# individuals	PGD		PGM		GDA	
			a	b	a	b	a	b
whole pop.	19	125	0.89	0.11	0.38	0.62	0.62	0.38
subpop. 1	3	6	0.58	0.42	0.00	1.00	0.33	0.67
subpop. 2	12	85	0.96	0.04	0.56	0.44	0.85	0.15
subpop. 3	4	34	0.91	0.09	0.12	0.88	0.13	0.87

Table 5. Within-colony relatedness and inbreeding coefficients for adult females. Estimates are given with standard errors. Brackets enclose 95% confidence intervals.

Species	Relatedness (<i>r</i>)	Inbreeding (<i>f</i>)
<i>M. basimacula</i>	0.435 ± 0.116 [0.186 to 0.683]	-0.105 ± 0.140 [-0.404 to 0.193]
<i>M. immarginatus</i>	0.766 ± 0.036 [0.691 to 0.841]	0.367 ± 0.066 [0.229 to 0.505]

Table 6. F-statistics for *Mischocyttarus*. Starred values are significantly greater than zero (one-tailed t-test). The subpopulations are clusters of nests usually located within 400 m of each other (see text).

species	statistic estimated	estimate ± s.e.	95% confidence interval
<i>M. basimacula</i>	F_{st}	-0.126 ± 0.133	-0.408 to 0.156
	F_{it}	-0.066 ± 0.016	-0.118 to -0.014
	F_{is}	-0.056 ± 0.160	-0.396 to 0.284
<i>M. immarginatus</i>	F_{st}	0.491 ± 0.089*	0.305 to 0.678
	F_{it}	0.437 ± 0.193	-0.392 to 1.000
	F_{is}	0.097 ± 0.143	-0.204 to 0.398

Table 7. Relatedness under the assumption of population subdivision. Starred values are significantly greater than zero (one-tailed t-test)

species	relatedness type	<i>r</i> ± s.e.	95% confidence interval
<i>M. basimacula</i>	r_{ct}	0.411 ± 0.114*	0.167 to 0.654
	r_{cs}	0.488 ± 0.121*	0.230 to 0.749
	r_{st}	-0.151 ± 0.061	-0.344 to 0.042
<i>M. immarginatus</i>	r_{ct}	0.828 ± 0.040*	0.745 to 0.911
	r_{cs}	0.584 ± 0.115 *	0.344 to 0.825
	r_{st}	0.586 ± 0.164 *	-0.118 to 1.000

ture. The point estimates of the F-statistics for *M. basimacula* are all slightly negative. The 95% confidence intervals for F_{st} and F_{is} show them to be consistent with zero values. Strangely, though the point estimate of F_{st} is quite close to zero, the confidence interval falls entirely below this value, suggesting that individuals tend to be slightly less similar to members of their own subpopulation (outside of their own colony) than they are to members of other subpopulations.

The inbreeding in *M. immarginatus* (high F_{st}) seems to be due to population subdivision (high F_{st}) with little contribution from inbreeding within the subpopulations (low F_{is}). This conclusion is not certain because while the point estimate of F_{st} is quite high, its 95% confidence interval includes zero. If

we conduct a one-tailed t-test of the reasonable a priori hypothesis that F_{st} is greater than zero, it is nearly significant ($0.05 < p < 0.1$).

Relatedness values are consistent with these findings (Table 7). Since there is little structure at the subpopulation level in *M. basimacula*, it is not surprising that relatedness to colony mates does not change much when estimated with respect to the subpopulation (r_{cs}) instead of with respect to the whole population (r_{ct}). Similarly, we should not expect individuals to be significantly related to subpopulation members other than their colony-mates (r_{ct}), and they are not.

More interesting results are expected for *M. immarginatus* since it does appear to be structured at the subpopulation level. Since some of the similarity within colonies can be attributed to a general similarity within subpopulations, relatedness within colonies is considerably lower when measured with respect to the subpopulation ($r_{cs} = 0.58$) than it is when estimated with respect to the whole population ($r_{ct} = 0.83$). Moreover, individuals appear to be closely related to members of their own subpopulation who are not colony-mates ($r_{ct} = 0.59$). This value is significantly greater than zero (one-tailed t-test).

Some observations bearing on this point were obtained during collection. Small active nests were sometimes located close to large and often inactive nests. Adults that we missed when collecting from active colonies would sometimes return to the inactive nest. This might indicate a general tendency of adults to move among nearby nests. Alternatively, it might be an indication of a specific past relationship with the abandoned colony, perhaps as a parent-colony.

DISCUSSION

Relatedness within colonies is fairly high in these two species of *Mischocyttarus*, in general agreement with results from *Polistes* (Metcalf and Whitt 1977, Lester and Selander 1981, Strassmann et al. 1989) and other primitively eusocial insects (Crozier et al. 1987; Schwarz 1987, 1988; Kukuk 1989; Ross and Matthews 1989). This means that worker behavior can be favored by kin selection without requiring extraordinarily high benefit-cost ratios (Hamilton 1964a,b, 1972). *M. basimacula* is in the low end of the range, and would therefore require a somewhat higher benefit-cost ratio than *M. immarginatus*, which is one of the species with highest relatedness, very near the outbred full-

sister value of $3/4$.

The two species differ markedly with respect to the presence of population substructure above the colony level, and this may have some consequences for relatedness. *M. basimacula* lacks both inbreeding and subpopulation differentiation. In fact the F_{st} is significantly negative, suggesting that a randomly chosen individual is more similar to members of other subpopulations than it is to members of its own subpopulation (excluding its own colony). We are unaware of any population process that might be operating to produce such an effect and suspect that this is a sampling effect; in a population with no substructure 1 in 20 samples will give a "significantly" negative F_{st} . In any event, the estimate is close enough to zero so that there is little effect on relatedness (compare r_{cs} and r_{ct}).

M. immarginatus does show some pronounced population structure. The population taken as a whole is quite highly inbred. F_{st} and f are high and significantly greater than zero (these two measures estimate essentially the same thing but differ because the latter is estimated under the assumption that there is structure at the subpopulation level). Since $1 - F_{st} = (1 - F_{cs})(1 - F_{ct})$, the inbreeding at the population level ought to be attributable to either population subdivision or to inbreeding within the subpopulations. Curiously, neither F_{st} nor F_{cs} is significantly different from zero, but the much higher point estimate for F_{st} suggests that population subdivision is responsible for the apparent inbreeding at the population level. Subpopulation structure has been detected in some other primitively eusocial insects. A very modest amount of differentiation has been found in a halictid bee (Crozier et al. 1987), a sphecoid wasp (Ross and Matthews 1989) and an anthophorid bee (Blows and Schwarz, pers. comm.). Highly differentiated subpopulations (separated by several kilometers) have been found only in *Polistes exclamans* (Viereck) (Davis et al. 1990). Three other *Polistes* species investigated in the same study showed no such differentiation.

Can *Mischocyttarus* tell us anything about the evolution of social traits like polygyny in the Epiponini? Itô (1984) has argued that some members of the *Mischocyttarus*, including *M. basimacula*, are polygynous. If this were true, *Mischocyttarus* and the Epiponini might have inherited the polygynous habit from a common ancestor. However, our study has revealed little evidence for true polygyny in *Mischocyttarus*. Some colonies had

more than one female with developed eggs, but the harmonic mean number of egg-layers was quite low. Moreover, relatedness in both species was too high to allow for very many egg-layers. Our data tend to support the conventional view that one female is usually able to dominate the others (Jeanne 1972; Litte 1977, 1979, 1981), perhaps with a minor amount of egg laying by subordinates.

In a different way, *M. immarginatus* seems to have a kind of population structure that could make it a suitable model for a species ancestral to the polygynous Epinonini. Polygyny tends to lower relatedness within colonies, which should increase selection for selfish behavior and could therefore erode the basis which maintains the structure of social insect colonies. This problem would be least likely to occur when polygyny arises in a species with initially high relatedness, due to single mating, inbreeding, or population viscosity. Of course this is not a barrier preventing polygyny from arising in species with low relatedness, but it could pose a barrier to the continued maintenance of worker behavior in such species. It should be noted that while *M. immarginatus* seems to have this suitable kind of population structure, two findings argue against the hypothesis. First, *M. basimaculata* does not have this kind of population structure and we do not know which species is more representative of the ancestor to the epinonines. Second, the three epinonine species that have been studied genetically show no inbreeding (Queller et al. 1988). These species were collected from areas as large as, or larger than, the area from which we collected *M. immarginatus*. Therefore, at least on this spatial scale, there seems to be no population subdivision in these three epinonines, and positing an ancestral population structure like that of *M. immarginatus* seems unnecessary. Further studies of *Mischocyttarus* and of additional epinonines might alter this conclusion.

The population subdivision in *M. immarginatus* makes the interpretation of relatedness coefficients more interesting and more complicated. If the subpopulations are reproductively isolated, then r_{cs} is the appropriate measure for predicting the average spread of altruism alleles within the subpopulations. The total population gene frequency does not enter into this measure if members of different subpopulations do not compete reproductively. However, this assumption seems unlikely. Although we have no direct evidence, it seems improbable that these subpopulations,

separated by less than 400 m, could be completely isolated.

If we assume that the subpopulations are not reproductively isolated, then r_{ci} may be the more appropriate measure for understanding the evolution of altruism among colony mates. Similarly r_{si} would be relevant to the evolution of altruism towards other members of the same subpopulation. However, three caveats must be added. First, since there is nonrandom mating, relatedness coefficients are exact only for social traits genes with additive dosage (Michod and Hamilton 1980; Seger 1981; Grafen 1985). Second, if the local subpopulation sizes are regulated independently, then success within subpopulations may translate non-linearly into success in the population as a whole. This is a special case of non-additive fitness components, a phenomenon that can make inclusive fitness models inexact (Cavalli-Sforza and Feldman 1978; Queller 1985). Finally, another complication arises if the similarity within subpopulations arises from pedigree connections more than a few generations back (Grafen 1985) because any new altruism allele would not experience the same structure shown by the marker alleles. However, this may not apply to *M. immarginatus*. Because the subpopulations are so close together, it seems most likely that the *M. immarginatus* subpopulations have been separated (probably partially) for only a very short time.

These caveats aside, the r_{ci} estimate shows that relatedness to female colony-mates is very high, closely approximating the full-sister value of 3/4. Relatedness to other members of the same subpopulation (r_{si}) is also quite high, so altruism towards individuals in other colonies could be favored. Whether such altruism occurs is unknown. Wasps that we had disturbed sometimes returned to other nests, suggesting some sort of connection between nests, but the new nests were usually abandoned or inactive.

The exact reason for the population structure is unknown. The simplest explanation is a strong tendency to begin new nests close to the natal nest. Several different patterns of this type have been reported from primitively eusocial polistine wasps. In *Polistes canadensis* (L.), multiple combs are constructed as part of a single colony with a single queen, and there is fluid movement of individuals among the combs (Jeanne 1979). This differs from *M. immarginatus* for several reasons. First, each comb had at least one female with developed ova-

ries. Second, having a single queen and fluid movement among nests should produce the same degree of relatedness between combmates and non-combmates, but we found the former to be higher. Finally, the combs in clusters of *M. immarginatus* were usually separated by at least 15 cm, compared to less than 3 cm in *Polistes canadensis*.

A more likely pattern that could lead to subdivision is the formation of satellite nests. In *Polistes exclamans*, females from an established nest may begin a new nest nearby, but connections between the parent and daughter nest are relatively ephemeral: movement of workers between them decreases and each has its own queen (Strassmann 1981a,b). Alternatively, simple philopatry may lead to the establishment of new nests near the site of the old inactive parent nest. This common pattern (Noonan 1981; Strassmann 1983) may also occur in *M. immarginatus* at another site in Mexico (Rodriguez 1989).

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A Revision of *Perissocentrus* Crawford (Hymenoptera:Torymidae)

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Abstract.—The South American genus *Perissocentrus* is revised. Six valid species are recognized: *P. argentinae* Crawford, *P. caridei* Brèthes, *P. chilensis* Crawford, *P. phormio* (Walker) (with *Monodontomerus vianai* Blanchard and *Megastigmus porteri* Brèthes as new synonyms), *P. striatulus* n. sp., and *P. tumidulus* n. sp. A neotype is designated for *P. caridei*. *Perissocentrus bruchi* Girault is transferred to the genus *Zaglyptonotus* Crawford. All species of *Perissocentrus* have been reared as parasites of lepidopterous pupae, but two species also are facultative hyperparasites of Ichneumonidae which attack the pupae.

The genus *Perissocentrus* Crawford is known from the Neotropical region between 10° north of the equator and 40° south. Five species were previously recognized. This is the first revision of the genus and it is based upon my study of type material and nearly 600 reared and collected specimens. I recognize 6 species as valid: *argentinae* Crawford, *caridei* Brèthes, *chilensis* Crawford, *phormio* (Walker) (with new synonyms *Megastigmus porteri* Brèthes and *Monodontomerus vianai* Blanchard), *striatulus* n. sp., and *tumidulus* n. sp. *Perissocentrus bruchi* Girault is transferred to the genus *Zaglyptonotus* Crawford. All species were reared as parasitoids of lepidopterous pupae, but 2 species were reported also as hyperparasites of ichneumonids attacking the pupae. It is possible that most, if not all, species act as facultative hyperparasites. Included in this paper is a host-parasite list (authors' names for hosts appear only in this list).

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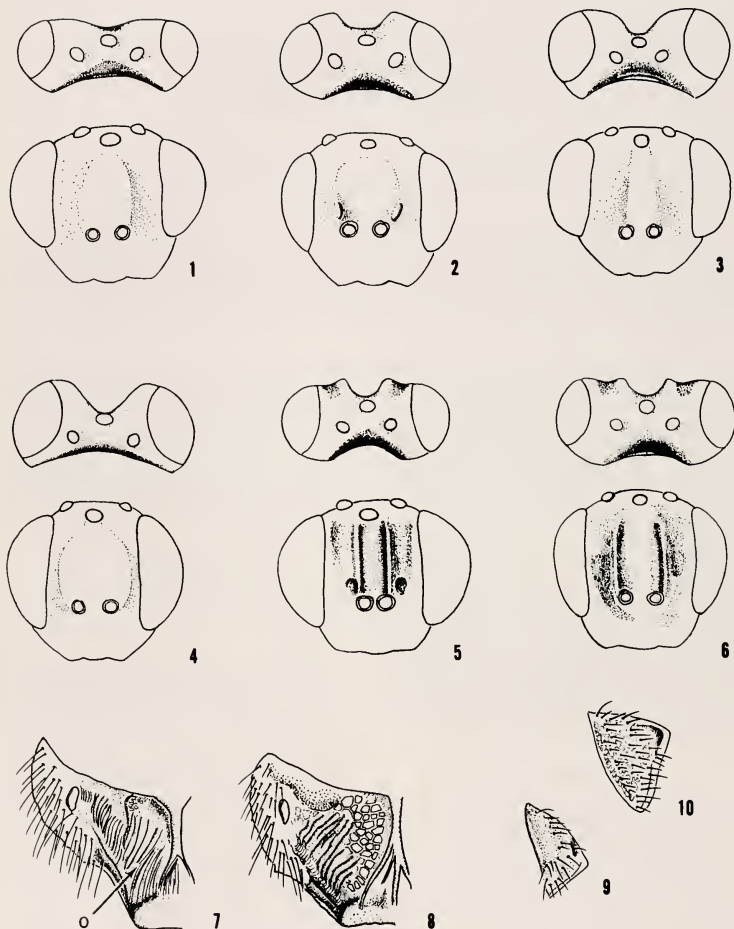
PERISSOCENTRUS Crawford 1910

Fig. 26, habitus

Perissocentrus Crawford 1910:235.

Type species: *Perissocentrus chilensis* Crawford. Original Designation.

Diagnosis.— Occipital carina (Fig. 18) present, ventrally joining hypostomal carina, placed mid-way between vertex and foramen; head in dorsal view transverse (Fig. 1-6, upper); antenna with first flagellomere (i.e. ring segment) reduced, much wider than long; antennal club 3-segmented; clypeal apex straight; marginal vein 4 to 5X longer than stigmal, postmarginal 2X longer than stigmal; frenal groove present; notauli complete; hindfemur with single, subapical tooth (Figs. 11-14) and sometimes with secondary distal lobe (Figs. 11-13); hindtibia (Figs. 11-14) straight, apex truncate, 2 hindtibial spurs inserted 1/5th or more distance from apex (Fig. 15), greatly elongate, the shorter one not extending much beyond hindtibial apex; propodeum projecting beyond metapleuron (Fig. 23), with well developed median carina (Figs. 7-8), sublateral foveae absent; hindcoxa setose dorsally;



Figs. 1-10. *Perissocentrus*. 1-6, Heads, frontal view (lower), dorsal view (upper). 1, *P. argentinae* (female). 2, *P. tumidulus* (male). 3, *P. phormio* (male). 4, *P. chilensis* (male). 5, *P. caridei* (male). 6, *P. striatulus* (male). 7-8, Propodea, left half, dorsal view (o = oblique carinae). 7, *P. striatulus*. 8, *P. caridei*. 9-10, Metapleuron, side view (left margin anterior). 9, *P. phormio*. 10, *P. argentinae*.

metasternum (Fig. 22) with hindcoxal foramen separated by sclerotized plate; metasomal tergum 2 posteriorly straight (Figs. 19-20).

Remarks.— Among torymid genera *Perissocentrus* and the monotypic Australian genus *Aloomba* Girault are the only two that have elongated hindtibial spurs which are located at least one-fifth or more the length of the hindtibia basad of the apex (Figs. 11-15). The condition of elongate spurs is known also in New World *Zaglyptonotus*, but in this genus the spurs are inserted at the apex of the tibia (Fig. 16) instead of proximally (Fig. 15). Modifications of hindtibial spurs also occur in *Platykula* Huber (Nearctic) and *Rhynchotica* Bouček (Afrotropical), but in these cases they are modified in thickness rather than length. There is one species of *Monodontomerus* (*M. strobili* Mayr) which has elongate spurs. I point this out as an indication that spur modification is a homoplasious character and does not necessarily indicate relationship.

Although *Perissocentrus* and *Aloomba* appear phenetically similar, they would not be confused at present because they occur in different zoogeographic regions. Alternatively, *Perissocentrus* and *Zaglyptonotus*, which occur in the same region, might superficially be confused because both have elongated hindtibial spurs. *Perissocentrus* differs in that the occipital carina is comparatively low on the head (Fig. 18) and ventrally contiguous with the hypostomal carina (high on the head and not reaching hypostomal carina in *Zaglyptonotus*, Fig. 17), the shorter of the two hindtibial spurs scarcely projects beyond the tibial apex (Fig. 15) (projecting much further in *Zaglyptonotus*, Fig. 16), metasomal tergum 2 is entire apically (Figs. 19-20) (emarginate

in *Zaglyptonotus*, Fig. 21), the propodeum is elongate (Fig. 23) (scarcely projecting beyond metapleuron in *Zaglyptonotus*, Fig. 25), and the metasternum is differently constructed, with the hindcoxal foramina separated from the anterior margin of the metasternum (Fig. 22) (touching margin in *Zaglyptonotus*, Fig. 24). The presence or absence of a frenal area and/or groove used by Crawford (1914) to separate the genera cannot always be relied upon because a few undescribed *Zaglyptonotus* (as defined above) have a faint frenal groove.

Perissocentrus appears to be most closely related to *Monodontomerus* and differs from it in two character states: the elongate and subapically placed hindtibial spurs (unmodified and apical in *Monodontomerus*) and the metasternum with the hindcoxal foramina separated from the posterior margin of the metasternum (Fig. 22) (touching margin in *Monodontomerus*, as for *Zaglyptonotus* Fig. 24). Both states found in *Perissocentrus* are hypothesized as apomorphic based upon my unpublished analysis, and my data indicate that *Perissocentrus* and *Monodontomerus* are sister taxa derived from a common ancestor and that *Perissocentrus* is the more specialized of the two taxa.

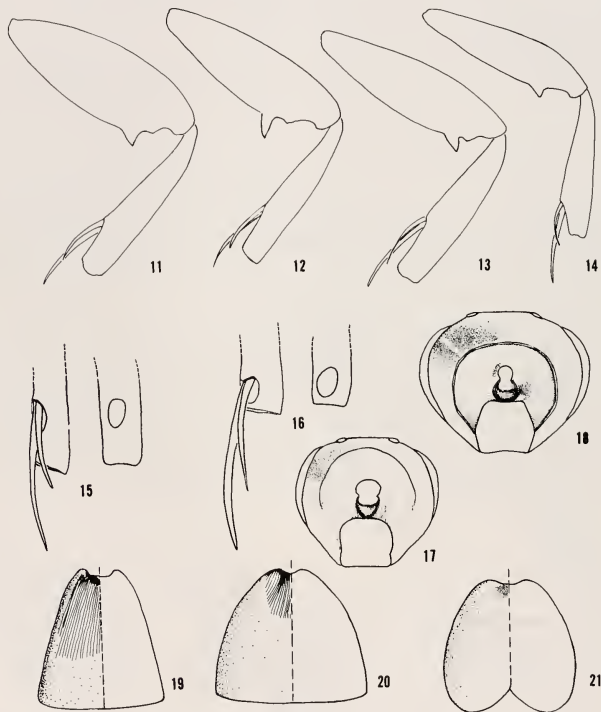
Perissocentrus, with 6 Neotropical species seems to replace *Monodontomerus* in that region. There are 2 known species of the latter genus in South America, but 10 to 15 species in the Nearctic.

Species of *Perissocentrus* display a remarkably broad array of characters and character states, and are sexually dimorphic for some of these states. The following key is artificial and not necessarily indicative of relationships.

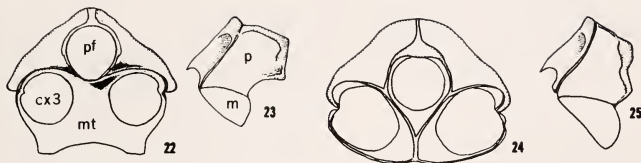
KEY TO FEMALE AND MALE PERISSOCENTRUS

1. Hindfemur with secondary lobe distad of ventral tooth (Figs. 11-13); 2
- Hindfemur without secondary lobe distad of ventral tooth (Fig. 14); 4
2. Metapleuron completely setose (Fig. 10); female scape yellow or yellow and green *argentinae* Crawford
- Upper metapleuron anteriorly without setae (Fig. 9); female scape entirely green 3
3. Scrobal depression reaching midocellus (Fig. 4); hindtibial spurs inserted 2/5 distance from distal apex (Fig. 13); female scape almost reaching ventral edge of midocellus; male without polished tumescence on lateral edge of scrobal depression above torulus (Fig. 4) *chilensis* Crawford
- Scrobal depression not reaching midocellus (Fig. 2); hindtibial spurs inserted 1/3 distance from distal apex (Fig. 12); in female, scape clearly not reaching ventral edge of midocellus; male with polished tumescence on lateral edge of scrobal depression above torulus (Fig. 2) *tumidulus* Grissell, n. sp.

4. Metasomal tergum 2 entirely polished; male with lateral margins of scrobal depression gradually curving onto frons which is neither sunken nor depressed (Fig. 3). *phormio* (Walker)
- Metasomal tergum 2 with basal 1/3 to 2/3 longitudinally striate (Figs. 19-20); male with scrobal depression laterally margined by raised border, frons sunken laterad of border (Figs. 5-6) 5
5. Frenal area and metapleuron (as in Fig. 10) entirely setose and sculptured; propodeum with incomplete posterolateral oblique carinae and anterolateral reticulation (Fig. 8). *caridei* Brèthes
- Frenal area asetose, medially polished; upper anterior area of metapleuron asetose (as in Fig. 9) and barely sculptured; propodeum laterally with oblique carinae (Fig. 7) and no reticulations. *striatulus* Grissell, n. sp.



Figs. 11-21. *Perissocentrus* and *Zaglyptonotus*. 11-14, Left hindfemur and tibia (outer view). 11, *P. argentiniae*. 12, *P. tumidulus*. 13, *P. chilensis*. 14, *P. phormio*. 15-16, Apex of hindtibia, side view (left), ventral view with apical spurs removed (right). 15, *P. caridei*. 16, *Z. mississippiensis*. 17-18, Heads, back view. 17, *Z. schwarzi*. 18, *P. tumidulus*. 19-21, Metasomal tergum 2, dorsal view (only left half showing sculpture). 19, *P. striatulus*. 20, *P. caridei*. 21, *Z. schwarzi*



Figs. 22-25. *Perissocentrus* and *Zaglyptonotus*. 22, 24, Thoracic metasternum, ventral view; cx3 = hindcoxal foramen; mt = metasternum; pf = propodeal foramen. 23, 25, Propodeum (p) and metapleuron (m), side view (right side posterior). 22-23, *P. tumidulus*. 24-25, *Z. schwarzi*.

***Perissocentrus argentineae* Crawford**

Figs. 1, 10, 11

Perissocentrus argentineae Crawford 1910:236. 3 female, 1 male syntypes, Ceres, Argentina. Lectotype female, USNM, herein designated.

Perissocentrus argentineae Brad.; Brèthes 1917b:374 (Fig. 11), 377. Erroneously attributed to "Bradford."

Diagnosis (both sexes except as noted).—Scape in female yellow or apical half green, in male entirely green, not reaching ventral edge of midocellus; scrobal depression obscure dorsally (Fig. 1), not reaching midocellus, sculpture varies centrally with some small polished areas surrounded by faint reticulation, setae continuous from sides of frons ventrad of midocellus, depression not deeply excavated in dorsal view (Fig. 1, upper), male depression unmodified on lateral edge above torulus; genal sulcus faint and visible only at some angles of view or only at base of eye; metapleuron covered with setae (Fig. 10), sculptured similarly overall; frenum without setae, sculptured similarly overall; hindfemur (Fig. 11) with secondary lobe distad of ventral tooth, hindtibial spurs inserted 1/3 distance from tibial apex; propodeum with few incomplete longitudinal carinae, surface nearly entirely reticulate; metasomal tergum 2 entirely polished; ovipositor 1.0 to 1.2 X length metasomal tergum 2.

Type Material.—*Perissocentrus argentineae* was described from the syntype series in USNM as noted above. All specimens bear the label data "Ceres, Argentina" and I designate one female lectotype with my handwritten label.

Material Examined.—In addition to the type material I saw 251 females and 162 males of this species from the following localities (all specimens USNM except as noted): ARGENTINA: 1 female, 1 male, San Javier (Prov. de Tucuman - locality not verified for this Province), I-1940, Bridarolli; 1 male,

San Martin (Prov. Mendoza), 9-XII-1967 on *Prosopis*; 19 females, 15 males, Tucuman (Prov. de Tucuman), XI-1953 (CNC); 225 females, 149 males, Buenos Aires (Prov. Buenos Aires), I-III-1958 and X-1949, some ex *Papilio polydamas* (CNC). CHILE: 1 female, Piscicultura (Aconcagua), 17-XI-1959 (CNC). URUGUAY: 4 females, 6 males, Pando, III-IV-1943, H. L. Parker, ex *Oiketicus* ?geyeri. BRAZIL: 1 female, "Pelotas," A. Ronna (MBR).

Distribution.—This species is known from Paraguay (De Santis 1979), southern Brazil (Parker et al. 1953), Uruguay, Chile, and northern Argentina.

Hosts.—*Perissocentrus argentineae* has been reported as a primary parasite of large Lepidoptera with emergence from the pupal stage. Parker, et al. (1953) reared *Perissocentrus argentineae* from an arctiid chrysalid (in Brazil) and from *Oiketicus* sp. (?geyeri) (Psychidae) from Uruguay. I examined these last-named specimens and confirmed the identity of the parasite. The host *Oiketicus platensis* was listed by Brèthes (1917a, 1917b, 1920b). I have seen several long series reared from *Battus polydamas* (Papilionidae, new host record).

Discussion.—*Perissocentrus argentineae* is unique among all species of the genus in having the hindfemur with a secondary lobe (Fig. 11) in combination with a completely setose metapleuron.

There is much confusion concerning this species in relation to *caridei*, and I discuss the problem and methods to separate them at some length under the latter species.

According to Crawford (1910), *P. argentineae* is the correct name for the species which Künckel (1905, 1908) called *Monodontomerus phormio* Walker in several papers on the biology of the species. There is no basis for Crawford's conclusion because he examined neither Walker's type nor Künckel's material. I have seen Walker's type (see discussion under *phormio*) and it is distinct from *P. argentineae*.

Because no specimens of Künckel's material were found, it is doubtful that anyone will be able to verify his identification.

Perissocentrus caridei Brèthes

Figs. 5, 8, 15, 20

Perissocentrus caridei Brèthes 1917a:340. **Nomen Nudum.**

Perissocentrus argentinæ var. *caridei* Brèthes 1917b:377-378. 1 female, 1 male syntypes, Argentina, destroyed. Neotype female, herein designated, MBR.

Perissocentrus caridei Brèthes; DeSantis 1967:185. **Revised status.**

Diagnosis (both sexes except as noted).—Scape in female yellow, in male green, not reaching venter of midocellus; scrobal depression reaching midocellus, evenly sculptured overall, asetose, relatively narrowly excavated in dorsal view, in male (only) margined by raised border laterally (Fig. 5, upper), frons sunken laterad of border and slight teardrop depression present on lateral edge of scrobal depression above torulus (Fig. 5, lower); genal sulcus absent or visible only at base of eye; metapleuron covered with setae, sculptured similarly overall (as for *argentinæ*, Fig. 10); frenal area scarcely perceptible as a region, completely setose and evenly sculptured; hindfemur without secondary lobe distad of ventral tooth (as in *phormio*, Fig. 14); hindtibial spurs inserted 1/5 distance from tibial apex (Fig. 15); propodeum with incomplete, posterolateral oblique carinae and anterolateral reticulation (Fig. 8); basal third of metasomal tergum 2 longitudinally striate (Fig. 20); ovipositor 1.3 to 1.5 X length metasomal tergum 2.

Type Material.—The problem of type material (and subsequent confusion with the species *P. argentinæ*) for this species is complicated, and the following discussion is given in the interest of nomenclatural stability. "*Perissocentrus caridei* n. sp." was mentioned by Brèthes without description in one paper (1917a:340), but was not described until a few pages later in a different paper in the same journal (Brèthes 1917b:377). Here he described it as "*Perissocentrus argentinæ caridei* n. var.," apparently from 1 female and 1 male as he gave only one length for each sex. No holotype was designated.

In searching for Brèthes' types, Dr. Jose Maria Gallardo (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia') was able to find only "a slide with dissected parts of the [incomplete] type."

This is labeled in Brèthes' handwriting with only the name and the word "type." Included on this slide are the mouthparts and one antenna of a male based upon the color of the scape. Because no holotype was selected in the description, and because the only remnant of the syntype series is a mandible and antenna, I am designating as lectotype for *P. argentinæ caridei* the illustration of the female given by Brèthes (1917b, Plancha III). The slide material of the male thus becomes a paralectotype. In ICZN Article 74(c) (1985) the statement is made that "designation of an illustration . . . of a syntype as a lectotype is to be treated as designation of the specimen illustrated." Since the lectotype specimen no longer exists, and since the circumstances of recognition of this species are exceptionally confused (see next paragraph), I follow ICZN Article 75(b)iii (1985) in designating a neotype in spite of the existence of a surviving paralectotype which, according to this section of the code, ". . . does not in itself preclude the designation of a neotype."

An argument cannot be made for designating a neotype based upon the supposition that syntypes are no longer extant because, in fact, parts of a syntype actually exist. Therefore one cannot use the "exceptional circumstances" argument (ICZN Article 75(b)ii) to overcome the problem of stability. The use of the illustration in this case is, in my opinion, the most viable option, within the parameter of the code, to settle the problem of stability.

The selection of a neotype is necessary because there is considerable confusion over what Brèthes really meant by the name "*caridei*." As previously mentioned, Brèthes listed *caridei* as a species (1917a) then described it as a variety of *argentinæ* (1917b). He realized that 2 taxa were present (1917b) because he gave habitus figures for both *argentinæ* (Plancha II) and *argentinæ* var. *caridei* (Plancha III). He repeated these figures again in 1920b (in which *caridei* is still referred to as a "n. var."). It is doubtful that Brèthes examined specimens of *argentinæ* described by Crawford, and we might presume that his concept of Crawford's species was based upon specimens taken from nearly the same localities (Crawford's from Santa Fe; Brèthes' from Cordoba and Buenos Aires).

In describing *caridei*, Brèthes did not mention differences between it and *argentinæ* so we must work from present knowledge to resolve the problem. The illustrations are not very helpful as they do not elucidate any diagnostic characters. Brèthes,

in 1918, identified some material from southern Brazil as *P. a. caridei*, and I borrowed these specimens through the courtesy of Dr. Gallardo (MBR). From these specimens and the type of *P. argentinae* Crawford, I conclude that *caridei* is a valid species and readily distinct from *argentinae* (I discuss these differences below, under the Discussion section).

In the interest of nomenclatural stability I herein designate a neotype from Brèthes' own material. It is selected from specimens mounted on two cards on the same pin; 4 female specimens are on the upper card and 4 females and 1 male on the lower card. The data label reads "E. Ronna, Pelotas." The neotype female is on the upper card with a black arrow pointing to it. It is in the MBR.

Material examined.— In addition to the above material I saw 3 female and 4 males as follows (all USNM): BRAZIL: 3 females, 2 males, Sao Paulo, 21-III-1942, H.L. Parker, ex Lepidoptera chrysalid ("?primaries"); 2 males, Mato grosso, 1934, J. Lane.

Distribution.— Reported in the literature from southern Brazil (De Santis 1980) and Uruguay (De Santis 1979) south to central Argentina (De Santis 1967). I can confirm only the Brazil records.

Hosts.— *Perissocentrus caridei* has been repeatedly listed as a parasite of *Oiketicus platensis* (Psychidae) (e.g., Brèthes 1917a,b, 1920b; Koehler 1939) and DeSantis (1967) gives also *Oiketicus geyeri* (Psychidae) and *Battus polydamas* (Papilionidae) as hosts.

Discussion.— As I pointed out above in the discussion of type material, the names *caridei* and *argentinae* have been confused since Brèthes' first description of *caridei*. In part this confusion exists because both species are reared from the same hosts, namely *Oiketicus platensis* and *O. geyeri*, and because they appear to have similar geographic distributions.

Perissocentrus caridei (both sexes) is the only species of the genus that has the frenal area entirely covered with setae (i.e., similar to remainder of scutellum); all other species have the frenum without setae. *Perissocentrus argentinae* has a few long recurved setae which project backward over the frenal area but they are situated in the frenal groove, never on the frenum itself. Additionally, *caridei* has only a single tooth on the hindfemur (as in *phormio*, Fig. 14) whereas *argentinae* has a prominent lobe distal to the tooth (Fig. 11). Further, *caridei* has metasomal tergum 2 with the basal third longitudinally striate (Fig. 20) whereas in *argentinae* metasomal tergum 2 is entirely smooth.

Havrylenko and Winterhalter (1949:44) provided a full page habitus drawing of *caridei* from Argentina, but it is so generalized that it could be any species of *Perissocentrus*.

Perissocentrus chilensis Crawford

Figs. 4, 13

Perissocentrus chilensis Crawford 1910:235-236. Number of specimens unknown, Santiago, Chile. Lectotype female, USNM, herein designated.

Diagnosis (both sexes except as noted).— Scape green, almost reaching venter of midocellus in female but not male; scrobal depression in female essentially parallel-sided and reaching midocellus, narrowly impressed (i.e., face between outer edge of depression and eye about as wide as scapal depression, as in Fig. 1 for *argentinae*), broadly impressed in male, i.e., face between outer edge of depression and eye narrower than width of scapal depression (Fig. 4), depression in both sexes essentially polished (very slight sculpture and a few setae may be detected below midocellus at magnification of 50X and above), scrobal depression distinctly impressed in dorsal view, male without modification on lateral edge above torulus; genal sulcus present; upper metapleuron anteriorly without setae (as in *phormio*, Fig. 9), sculptured similarly overall; frenum without setae, faintly reticulated sculptured overall (may appear shiny in some views); hindfemur (Fig. 13) with secondary lobe distad of ventral tooth; hindtibial spurs inserted 2/5 distance from apex; propodeum with complete longitudinal carinae, intercarinal surfaces smooth; metasomal tergum 2 entirely polished; ovipositor 0.9 to 1.1X length metasomal tergum 2.

Type Material.— The number of specimens used for the original description was not given by Crawford (1910). Twelve syntypes (7 females, 5 males) from Santiago, Chile now reside in the USNM collection, and I designate by label 1 female as lectotype.

Material examined.— In addition to the type material I saw 13 females, 11 males all from CHILE as follows: 1 female, Colina (El Portezuelo), XI-1978 (USNM), 11 females, same, coll. III-1988, 5-IV-15-V-1988, L. E. Peña (CNC); 1 female, Fundo Malcho, 11-20-XI-1964, L. E. Peña (CNC); 8 males, rd. to Ovalle, 17-II-1985, I. Gauld (CNC); 2 males, Aysen, Chico, 24-31-XII-1960, L. E. Peña (CNC), 1 male, Chovellen, Maule, 5-XII-1953, L. E. Peña (CNC).

Distribution.— Known only from Chile.

Hosts.— This species was described originally from the saturniid *Ormiscodes crinita* (now = *cinnamomea*) (Saturniidae). De Santis (1979) also recorded the hosts *Cercophora* (= *Cercophana*) *frauenfeldii* (Saturniidae) and *Thanatopsyche chilensis* (Psychidae). I have not verified these last hosts.

Discussion.— *Perissocentrus chilensis* is defined by the combination of hindfemur with a secondary lobe, the upper metapleuron anteriorly without setae, and the scrobal depression which reaches the midocellus. In addition to the key characters cited above, *P. chilensis* is separated from *P. tumidulus* by the ovipositor which is at most 1.1X the length of metasomal tergum 2 (over 1.5X as long in *tumidulus*).

***Perissocentrus phormio* (Walker)**

Figs. 3, 9, 14

Torymus phormio Walker 1843:113. Lectotype female, Valparaíso. BMNH, examined.

Monodontomerus phormio (Walker); Künckel 1905:227-228. Generic transfer.

Perissocentrus phormio (Walker); Bouček 1983:2. Generic transfer.

Megastigmus porteri Brèthes 1916:9. 1 female, 1 male syntypes, Santiago, Chile. ?MBR, presumably lost. **NEW SYNONYMY.**

Perissocentrus porteri (Brèthes); Brèthes 1920a:15. Generic transfer.

Monodontomerus vianai Blanchard 1936:7-9 (Fig. 1a-d). Number of syntypes unknown, "provincia Salta." [Types reported in Blanchard's collection and the entomology laboratory of the "División de Zoología Agrícola del Ministerio de Agricultura de la Nación", not found.] **NEW SYNONYMY.**

Diagnosis (both sexes except as noted).—Scape green, not reaching venter of midocellus; scrobal depression reaching midocellus, centrally polished from torulus nearly to midocellus (may be small triangular patch of sculpture ventrad of ocellus), in female relatively narrowly excavated in dorsal view, in male (Fig. 3) lateral margins not bordered but gradually curving onto frons which is not sunken or depressed and without modification on lateral edge above torulus; genal sulcus present but faint and visible only at some angles of view; upper metapleuron anteriorly without setae, polished (Fig. 9); frenum without setae, sculptured but medially nearly polished; hindfemur (Fig. 14) without secondary lobe distad to ventral tooth; hindtibial spurs inserted 1/4 distance from tibial apex; propodeum with complete longitudinal carinae, intercarinal surfaces smooth; metasomal tergum 2 entirely polished; ovipositor 1.2 to 1.5 X length metasomal tergum 2.

Type Material.— *Torymus phormio* was apparently described from one specimen, designated as lectotype by Z. Bouček in BMNH (Hym. Type 5.54). The syntypes of *Megastigmus porteri* Brèthes have not been found in MBR, but J.M. Gallardo of that museum has sent 2 females from Santiago, Chile (the type locality) which are identified by Brèthes as "*Perissocentrus porteri* (Brèthes) Brèthes." These are apparently the specimens which Brèthes (1920a) used to transfer the specimens from *Megastigmus* to *Perissocentrus* and I used them as the basis for my interpretation of *P. porteri*. *Monodontomerus vianai* Blanchard was described from an unspecified number of females and males collected by Viana. Attempts to locate these specimens proved unsuccessful, but in the collection of FCNM are 2 females and 1 male (on a single pin) collected by Viana and labeled as "*Monodontomerus vianai* n. sp. Blan." These specimens come from the province of "BsAs" (= Buenos Aires) and not Salta as specified in the original description. I have used these specimens as the basis for my interpretation of *M. vianai*.

Material examined.— In addition to the types, I have seen 15 females and 5 males from the following localities (all specimens USNM except as noted): BOLIVIA: 1 female, 1 male, (no locality), XII-1972; B. Rose, with *Melipotis* material. CHILE: 1 female, 1 male, La Rosa, IX-1952, O. Higgins, secondary parasite of *Cirphis* (= *Leucania*); 1 female, Los Trancas (Andes Range), 20-25-II-1980; 1 female, Castro, 12-XII-1940, P. A. Bery, on *Ormiscodes*; 1 male, Las Cruces, V-1961, N. Krauss; 1 female, Las Cruces, X-1958, L. E. Peña (CNC); 1 female, 1 male, Valdivia, 19-I-1974, J. Naray, hyperparasite of *Ichneumonidae*; 1 female, Rio Bio Bio, 2-6-I-1959 (CNC); 2 females, Fundo Malcho, XII-1957, L. E. Peña (CNC); 1 female, Arauco, 20-28-I-1959, L. E. Peña (CNC); 1 female, 8 km. down from Termas Chillan, 16-I-1985, I. Gauld (CNC); 1 female, 48 km. along Santiago-Disputada rd. 9-I-1985 (CNC); 2 females, rd. to Ovalle, 17-II-1985, I. Gauld (CNC); 1 male, 14 km. up Anihuanagui rd., 26-I-1985, I. Gauld (CNC). ARGENTINA: 1 female, Buenos Aires, 23-X-1919, J. Brèthes (MBR); 2 females, Plumerillo (Prov. Mendoza), 20-X-1968, ex *Oiketicus platensis* (FCNM).

Distribution.— This species occurs from Bolivia to south-central Chile and Argentina.

Hosts.— Based upon examined specimens this species is associated with *Oiketicus platensis* (Psychidae), *Leucania* and *Melipotis* (Noctuidae), and

Ormiscodes (Saturniidae) and is, as well, a secondary parasite on ichneumonids. This species is reported in the literature as a parasite of *Orgyia antiqua* (Lymantriidae) by Brèthes (1920a:15), Pairon (1944:140), and Etcheverry and Ramírez (1964:65). Künckel (1905:227-228; 1908:231) reported this species from *Psyche* (= *Lumaca*) *künckeli* (Psychidae), but there is no way to ascertain if the specimens were correctly identified. [Crawford (1910:236) stated that Ashmead made this identification, but Ashmead most likely had never seen Walker's type.] Hosts reported for the type specimens of *P. vianai* (Blanchard 1936) were the ichneumonid *Paraepichthis bazani* and the noctuid *Alabama argillacea*.

Discussion.— This species is recognized by the character combination of the hindfemur without secondary lobe and metasomal tergum 2 entirely polished. *Perissocentrus phormio* and *chilensis* are similar in appearance and might easily be confused if the hindfemur is badly positioned. In these cases, *phormio* is recognized by the insertion point of the hindtibial spurs being relatively closer to the apex of the tibia (Fig. 14) than in *chilensis* (Fig. 13). *Perissocentrus phormio* appears to be the most primitive member of the genus based upon both the single femoral tooth and the unmodified metasomal tergum.

***Perissocentrus striatulus* Grissell, new species**

Figs. 6, 7, 19, 26

Description of female holotype (paratype variation enclosed in brackets).— Body length 3.1 mm (3.8 mm with ovipositor) [3.2–5.2 mm with ovipositor]; body metallic greenish black, including scape, except as follows: orange are apices of fore and midfemora, tibiae except faintly metallic green medially on outer side [may be entirely orange], tarsi (except mid and hindbasitarsi whitish); brown are flagellum, wing veins, ovipositor sheaths; scape not reaching venter of midocellus; scrobal depression not reaching midocellus, centrally polished (sculpture and setae continuous from sides of frons ventrad of ocellus), shallowly excavated as in *argenteae* (Fig. 1) with depression about as wide as distance between its lateral edge and eye; genal sulcus absent; upper metapleuron anteriorly without setae, slightly sculptured; frenum without setae, medially polished; hindfemur without secondary lobe (as in Fig. 14 for *phormio*) distad of ventral tooth; hindtibial spurs inserted 1/5 distance from tibial apex; propodeum laterally (Fig. 7)

with complete oblique carinae, intercarinal surfaces smooth, no reticulations present; basal 2/3 [2/3 to 3/4] of metasomal tergum 2 (Fig. 19) longitudinally striate; ovipositor 1.4 [1.3 to 1.5] X length metasomal tergum 2.

Male.— Differs from female as follows: body length 1.7–3.3 mm; scape exceeding midpoint of midocellus; scrobal depression reaching venter of midocellus (Fig. 6) margined laterally by raised border caused by frons sunken laterad of edge, lower face without modification on lateral edge above torulus, noticeably depressed laterally in large specimens, less obvious in small ones.

Type Material.— Holotype female, Colombia, Cundinamarca, Zipaquirá, 10-IX-1966, L. Pasada, secondary parasite of geometrid on pine (deposited in USNM); 46 female, 45 male paratypes as follows (in USNM unless otherwise specified): 27 females, 23 males, same data as holotype (3 females, 3 males each deposited in CNC, BMNH); 15 females, 20 males, Colombia, Boyacá, Tunja, 1971, H. E. Lugo, secondary parasite of Lepidoptera on pine (2 females, 2 males each deposited in CNC, BMNH); 1 male, Colombia, Narino, Pasto, December 1986, M. Hernandez, ex pupa *Cyanotricha necyria*; 1 female, Ecuador, Pichincha, Quito, II-1984, E. Martinez, secondary parasite of *Casinaria cavigena* on *Leuculopsis pulverulenta* (on *Pinus radiata*); 3 females, 1 male, Ecuador, Salcedo, IV-1985, G. Taniguchi, ex pupa *Cyanotricha necyria*.

Distribution.— In the Andean range from north central Colombia (Tunja) to central Ecuador (Salcedo).

Hosts.— This species has been reared from a pupa of *Cyanotricha necyria* (Dipteridae) and as a secondary parasite of *Casinaria cavigena* (Ichneumonidae) on *Leuculopsis pulverulenta* (Geometridae). The majority of records indicate that this species is a secondary parasite.

Etymology.— From the Latin "stria," in reference to the longitudinal striations on metasomal tergum 2.

Discussion.— Only *P. striatulus* and *P. caridei* share the condition of a striate second metasomal tergum (both sexes). Additionally, males are unique in the genus by having well-defined, parallel-sided scrobal depressions with the area between the edge and the eye depressed. In addition to characters given in the key, males of *P. striatulus* may be distinguished from those of *P. caridei* by the absence of a small depression just laterad of the toruli (Fig. 6) (present in *caridei*, Fig. 5).



Fig. 26. *Perissocentrus striatulus* n. sp. Habitus.

***Perissocentrus tumidulus* Grissell, new species**

Figs. 2, 12, 18, 22, 23

Description of female holotype (paratype variation enclosed in brackets).— Body length 3.3 mm (4.1 mm with ovipositor) [3.3 - 4.6 mm with ovipositor]; body metallic greenish black, including scape, except as follows: burnt-orange are fore- and midfemur [to mostly metallic green], tibiae except faintly metallic green on outer side, tarsi (except mid and hindbasitarsi whitish); brown are flagellum, wing veins, ovipositor sheaths; scape not reaching venter of midocellus; scrobal depression obscure dorsally, not reaching midocellus (setae continuous from sides of frons ventrad of midocellus) [sculpture varies centrally with some small polished areas surrounded by faint reticulation], scrobal depression shallowly excavated in dorsal view but lateral margin above torulus slightly

bulging, especially in lateral view; genal sulcus faint and visible only at some angles of view or only at base of eye; upper metapleuron anteriorly with narrow asetose area, sculptured similarly overall; frenum without setae, weakly sculptured similarly overall (appearing shiny in incandescent light); hindfemur (Fig. 12) with secondary lobe distad of ventral tooth; hindtibial spurs inserted $1/3$ distance from apex; propodeum with weakly developed longitudinal carinae, intercarinal areas weakly reticulate; metasomal tergum 2 entirely polished; ovipositor 1.5 [1.5 to 1.8] X longer than metasomal tergum 2. [Propodeum (Fig. 23) and metasternum (Fig. 22) illustrated to demonstrate generic characters.]

Male.— Differs from female as follows: body length 2.5 - 2.7 mm; scrobal depression with polished tumescence on lateral edge above torulus (Fig. 2).

Type Material.—Holotype female, Chile, Cautin, Temuco, 1945, G. O. Faure, ex butterfly (deposited in USNM); 20 female, 9 male paratypes all from Chile as follows: 7 females, 2 males (including allotype) same data as holotype; 1 female, LaCruz, V-1963, ex "*Tanatopsyche*" (= *Thanatopsyche*) *chilensis*, S. R. Poblete (USNM); 8 females, 5 males, LaCruz, III-1971, S. Rojas, ex *Cercophora* (= *Cercophana*) (1 female, 1 male USNM, 7 females, 4 males CNC); 3 females, 2 males, Santiago, 15-30-VIII-1942, L. Duran, ex *Thanatopsyche chilensis* (USNM); 1 female, Santiago, 1942, H. Pairó, ex cocoon *Thanatopsyche chilensis* (USNM).

Distribution.—Known only from central Chile, from Santiago south to Cautin.

Hosts.—The species has been reared from *Thanatopsyche chilensis* (Psychidae) and *Cercophana* sp. (Saturniidae).

Etymology.—From the Latin "tumeo," in reference to minute swellings on the face of males of this species.

Discussion.—*Perissocentrus tumidulus* and *P. chilensis* are likely to be confused because they are reared from similar hosts (psychids and saturniids), are sympatric, and appear similar structurally. Males of both species are easily separated based upon the face. Not only does *P. tumidulus* have the polished elevations just above the toruli (Fig. 2; absent in *P. chilensis*, Fig. 4), but the scapal depression does not continue to the midocellus and the side of the face between the depression and the eye is wide compared to that of *P. chilensis* which is very narrow (Fig. 4). Females of both species can be separated by characters given in the key, but these are sometimes difficult to see (especially the scapal depression which may be covered by the scapes. In addition to the key characters given for females, the tooth of the hind femora of *P. tumidulus* is relatively longer, more robust, and more distinctly right-angled (Fig. 12) than that of *P. chilensis* (Fig. 13), but again this is somewhat difficult to appreciate without both species for comparison. Females may also be separated by the ovipositor which is longer (about 1.5X) than metasomal tergum 2 in *P. tumidulus*, but at most 1.1X longer than metasomal tergum 2 in *P. chilensis*.

SPECIES REMOVED FROM *PERISSOCENTRUS*

***Zaglyptonotus bruchi* (Girault), new combination**

Perissocentrus bruchi Girault 1917:11-12. Holotype female, "from *bruchii* P.C. 55/5." USNM, examined.

Discussion.—There is no doubt that this species should be placed in the genus *Zaglyptonotus* based upon the synapomorphy of the elongated hindtibial spurs inserted at the apex of the tibia. Additional characters that place this species in *Zaglyptonotus* are the occipital carina placed relatively high up on the head and not meeting the hypostomal carina, the propodeal and metasternal structures, and the emarginate metasomal tergum 2. The cryptic label data "from *bruchii* P. C. 55/5" have never been explained and no type locality has been ascertained although a number of gazetteers have been studied. In addition, I have asked Spanish, Portuguese, and Italian speaking entomologists if they can make sense of the label and none have. The paper by Girault treats species from the United States, Mexico, Africa, Ceylon, and Europe so there is no evidence of locality from the paper itself.

De Santis (1989) reported this species (as *Perissocentrus*) from Argentina as a parasite of Bruchidae in seed pods of *Prosopis argentinae*. I have seen the specimens (from FCNM) upon which this identification was based and compared them with the type of *bruchii*. I can confirm that they are correctly identified to species. The species name "*bruchii*" was obviously derived from the label name "*bruchii*" on the type label and it is possible that this was a common name for Bruchidae.

This is the first record of *Zaglyptonotus* from the Neotropical region. Other Neotropical species occur there because I have seen specimens (including undescribed species) in the USNM from Colombia, Brazil, Chile, and Argentina. The 2 known U.S. species range into Southmost, Texas, but have not yet been reported further south.

HOST-PARASITE LIST FOR *PERISSOCENTRUS*

LEPIDOPTERA

Arctiidae:

Arctiid chrysalid: *Perissocentrus argentinae*

Dioptriidae:

Cyanotricha necyria Felder: *Perissocentrus striatulus*

Geometridae:

Leucolopsis pulverulenta Dognin: *Perissocentrus striatulus*

Lymnariidae:

Orgyia antiqua (L.): *Perissocentrus phormio*

Noctuidae:

Alabama argillacea Hübner: *Perissocentrus phormio*

Leucania sp.: *Perissocentrus phormio*

Melipotis sp.: *Perissocentrus phormio*

Papilionidae:

Battus polydamas (L.):

Perissocentrus argentinae,

Perissocentrus caridei

Psychidae:

Lumacra kunkeli (Heylerts): *Perissocentrus phormio*

Oiketicus geyeri Berg: *Perissocentrus caridei*

Oiketicus ?geyeri Berg: *Perissocentrus argentinae*

Oiketicus platensis Berg:

Perissocentrus argentinae,

Perissocentrus caridei,

Perissocentrus phormio

Thanatopsyche chilensis (Philippi):

Perissocentrus chilensis,

Perissocentrus tumidulus

Saturniidae:

Cercophana frauenfeldii Felder: *Perissocentrus chilensis*

Cercophana sp.: *Perissocentrus tumidulus*

Ormiscodes cinnamomea (Guerin-Meneville):

Perissocentrus phormio

Ormiscodes crinita Blanchard see *Ormiscodes cinnamomea*

Ormiscodes sp.: *Perissocentrus phormio*

HYMENOPTERA

Ichneumonidae:

Casinaria cavigena Walley: *Perissocentrus striatulus*

Paraepchthis bazani Blanchard: *Perissocentrus phormio*

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**Collecting *Aphelinus* spp. (Hymenoptera: Aphelinidae)
in Southwestern CIS for "Pre-emptive" Biological Control of *Diuraphis noxia*
(Homoptera: Aphididae) in Australia**

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Abstract.—Surveys of wheat and barley fields were conducted in 1989 and 1990 in parts of Ukraine, southern Russia, and Georgia (CIS), aimed at discovering *Aphelinus* spp. parasitoids of *Diuraphis noxia*. Enough mummies could be collected and shipped in both years to allow for the entomophage to be mass-reared and field-released in Australia as part of a "pre-emptive" integrated control program, i.e. before this aphid has even reached the continent.

Over the last decade, the Russian wheat aphid (RWA), *Diuraphis noxia* Mordwilko (Homoptera : Aphididae) has become a major pest of wheat and barley in southern Africa and North America (Evans et al. 1989). Australia is now the main grain exporting country without RWA, and Hughes and Maywald (1990) have demonstrated that its accidental introduction would result in severe losses to cereal crops over a large proportion of the Australian wheat and barley growing area. To minimize the likely economic consequences of RWA introduction into Australia, a national management plan has been developed to coordinate responses to the pest's arrival. This attempt represents the first concerted program of "pre-emptive" integrated control (Evans et al. 1989) against an arthropod pest. It involves in particular research in biological control, determination of the adequate use of insecticides, as well as a comprehensive screening and breeding program for host plant tolerance or resistance (Martinelle et al. in press a; b).

The classical component of the plan aimed at selecting species of natural enemies of *D. noxia* for introduction into Australia based on the following criteria : (1) ability to attack the host aphid in its cryptic feeding niche ; (2) aptitude to complete development on some of the exotic grass aphid species that are already distributed in the Australian agroecosystems ; (3) faculty to survive under extreme climatic conditions equivalent to those of the Australian wheat belt.

Among the various parasitoid species recorded from cereal aphids (cf. Stary 1981 for instance), and

in particular from RWA, representatives of the genus *Aphelinus* Dalman (Hymenoptera: Aphelinidae) fulfill the three above requirements. According to Z.L. Berest (pers. comm.) chalcids only are capable to efficiently attack RWA colonies developing in rolled leaves of cereal plants. Also *Aphelinus* spp. have been reported during 1976-79 as the most important entomophages of *D. noxia* close to its probable centre of origin (Berest 1980). As a consequence, a search for suitable *Aphelinus* spp. and the screening for wheat and barley cultivars showing signs of resistance to various biotypes of RWA were undertaken simultaneously from 1989 on by the Montpellier (France) Biological Control Unit of CSIRO's Division of Entomology. This paper summarizes results obtained in relation with the first aspect of this research program only, i.e. with its component of classical biological control.

SURVEY AND COLLECTION

Numerous wheat and barley fields were visited in May-June 1989, and again during the same period of 1990. These were situated in the Ukraine (along a transect Uzhgorod-Kiev-Odessa, and along the Black Sea coast), southern Russia (Cherkessk-Nalcik-Budennovsk, north of the Caucasus), and Georgia (Abkhazia, south of the Caucasus). The various techniques used for assessing the aphid populations and the impact of their natural enemies, as well as the materials used for preparing and shipping mummies of the selected ento-

mophagous species were as described in detail by Aeschlimann and Vitou (1985).

Throughout the whole area of investigation aphid numbers on average rarely exceeded 1 individual per stem, RWA being almost absent from both cultivated and volunteer species of Gramineae in 1989 and 1990, from sea level to over 2000 m altitude. A totally different situation, however, was observed in experimental gardens where the regional or national Plant Breeding Institutes maintained their collections of cultivars and local accessions. These were usually planted several weeks later than regular crops nearby, and scientists in charge of the station tried to avoid any applications of pesticides. Under those circumstances, spring barley and, to a lesser extent spring wheat harboured very dense aphid infestations (often several hundred individuals per stem), which apart from *D. noxia* comprised large proportions of *Rhopalosiphum padi* Linnaeus, *Schizaphis graminum* Rondani, and *Sitobion avenae* Fabricius (Homoptera: Aphididae). During the 1989 and 1990 visits, 10.9 % of the colonies on average were RWA alone, and 81.4 % mixed populations of two or more aphid species in the Odessa district (Ukraine). Also, it is worth emphasizing that *D. noxia* colonies comprised more individuals and occurred in higher numbers per plant at plots located at the edge of the fields as compared with those situated in the centre of the garden. The highest RWA infestations were observed at spring barley plots adjacent to uncultivated land in which volunteer representatives of *Aegilops* Linnaeus were found at low density, suggesting a possible association with this genus, closely related genetically to *Triticum* Linnaeus.

In the experimental fields of the All-Union Institute for Plant Breeding and Genetics at Odessa, the absolute numbers of aphid mummies recorded per sampling day were similar to that of cadavers showing signs of infection by Entomophthoralean fungi (Zygomycetes: Entomophthorales). Each of those two categories (parasitized and infected aphids) represented an estimated 5 % of the total number of live aphids occurring on the host plants on average of both sampling periods. The overall frequency distribution of natural enemies (relative importance in Table 1) was based on the total number of mummies recorded during the whole collecting time. Results for the various species of the genera *Aphelinus* and *Aphidius* are therefore pooled in Table 1 below, as no distinction could be

Table 1. Relative importance of the entomophagous species of *Diuraphis noxia* in southwestern CIS, 1989-90.

Parasitoid species (1)	Relative importance within the parasitic complex (%)
1. Hymenoptera: Aphelinidae <i>Aphelinus</i> ? <i>asychis</i> Walker <i>Aphelinus varipes</i> Foerster	0.5
2. Hymenoptera: Aphidiidae <i>Aphidius ervi</i> Haliday <i>Aphidius matricariae</i> Haliday <i>Aphidius rhopalosiphi</i> De Stefani-Perez <i>Aphidius uzbekistanicus</i> Luzhetzki	44.8
<i>Diaeretiella rapae</i> M'Intosh	2.0
<i>Ephedrus plagiator</i> Nees	0.2
<i>Praon volucre</i> Haliday	52.5

(1) Importance assessed in terms of numbers of mummies, i.e. to generic level only.

made between mummies of the different species of each of those two genera. Adult parasitoids emerging "en route" (cf Aeschlimann and Vitou 1985) were identified by P. Stary (Aphidiidae) and M. Carver (Aphelinidae), voucher specimens being kept at CSIRO Montpellier (first author) and CSIRO Canberra (M. Carver).

As Table 1 clearly indicates, *Aphelinus* spp. appeared to have less impact on RWA populations developing in island-type situations than under outbreak conditions (cf. Berest 1980). As a consequence, some 25 hours field work were necessary on total each year to obtain enough viable mummies of the chalcid parasitoids to successfully initiate a mass-production in Australia. Both in 1989 and 1990, starter cultures were hand-carried from the Odessa sites and safely forwarded from Montpellier (France) to CSIRO quarantine facilities at Canberra (Australia) in less than 5 days. After the prescribed quarantine propagation, *Aphelinus varipes* Foerster was released as from the second half of 1990 in south-east Australia, where first signs of establishment have been observed and its dispersal and incidence in the fields are being monitored (R.D. Hughes and L.T. Woolcock pers. comm.).

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RESUME

Récoltes de parasitoïdes de *Diuraphis noxia* (Homoptera : Aphididae) dans le sud-ouest de la CEi, dans le cadre d'un programme de lutte biologique "préventive" en Australie.

Au cours de prospections sur cultures de blé et d'orge menées en Ukraine, Russie méridionale et Géorgie (CEi), des momies d'*Aphelinus* spp. (Hymenoptera : Aphelinidae) ont pu être récoltées et envoyées en nombre suffisant pour constituer un élevage aux fins de libération en Australie. On décrit ici le premier exemple de protection intégrée "préventive", c'est à dire dirigée contre un arthropode nuisible avant même qu'il n'ait envahi une aire biogéographique.

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**Taxonomic and Bionomic Observations on a Floridian
Panurgine Bee, *Perdita (Hexaperdita) graenicheri* Timberlake
(Hymenoptera: Andrenidae)**

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Abstract. — *Perdita (Hexaperdita) graenicheri* Timberlake is a solitary, gregarious, ground-nesting bee. It is more variable in color and male morphology than recognized previously. Males exhibit strong positive allometry in the relative size of a genal tubercle, in mandible length and width, and in length of the vertex. The species is believed to be univoltine with protracted emergence from late July to early November. Nest architecture and provisioning behavior are described, along with notes on immature stages. Relatively lengthy matings, 5-12 min., occur on flowers of *Heterotheca subaxillaris*, the pollen source. Information on plant hosts and associated insects is also provided.

Perdita is a monophyletic genus containing 769 named species and subspecies, ranging from southern Canada to Central America, with the apparent center of species diversity in the southwestern United States and northern Mexico (Hurd 1979, Ruz 1987, Rozen and McGinley 1988). These relatively small, panurgine bees are highly oligolectic (Linsley 1958).

Seventeen species of *Perdita* occur in Florida, six of which are restricted to the state, including *P. graenicheri* (Mitchell 1960). Many Floridian plants and animals reflect western affinities (Hubbell 1961), and the eastern *Perdita* are found primarily in sandy areas of the southern coastal plain (Mitchell 1960). Deyrup (1989) noted that many species of Florida arthropods have close relatives in the southwestern U.S., Mexico, and Central America. He suggested that this pattern provides evidence of an ancient continuous austral band of xeric habitat. The Florida peninsula today contains a series of inland sand ridges that functioned as biotic refuges during Miocene, Pliocene, and Pleistocene inundations (Neill 1957).

MATERIALS AND METHODS

Study Site.—Field work was done at the Archbold Biological Station, Highlands County, Florida, 8-14 August (BBN, KVK) and 28 December 1989 (BBN). *Perdita graenicheri* occurred at several of the terrestrial habitats at the Station, particularly in the sand pine scrub and southern ridge sandhill associations. Nesting data were obtained and many floral visits and matings were observed in the sand

pine scrub adjacent to the northeastern end of Lake Annie. Additional matings and floral visits were observed in the southern ridge sandhill area.

Bees nested in sunny, exposed patches having sparse vegetation (Fig. 1). Nesting substrate consisted of loose, small-grained, white quartz sand and particles of charred organic residue accumulated over years of scrub fires. All nests occurred in horizontal or slightly sloping areas where the sand was well drained, but moist just below the surface.

Voucher Material.—Specimens of *P. graenicheri* from this study are deposited in National Museum of Natural History, Smithsonian Institution (USNM), Archbold Biological Station, American Museum of Natural History, and Snow Entomological Museum. Specimens of the bee host plants, *Heterotheca subaxillaris* and *Chrysopsis microcephala*, are deposited in the U.S. National Herbarium (USNM).

Morphometrics.—Morphometric analysis of male head allometry was based on measurements of 41 specimens collected at the Archbold Biological Station in 1986 by M. Deyrup and in 1989 by KVK and BBN. Eight linear measurements (6 head and 2 thoracic, Fig. 2) were made with a binocular microscope equipped with an ocular micrometer. Means are given \pm standard error of the mean (SEM).

Allometric relationships were calculated using reduced major axis regression of log-transformed data (Shea 1985, LaBarbera 1989). A multivariate estimate of overall size was first calculated for each specimen as the score on the first principal components axis, when the original eight variates were

Fig. 1. Sand road adjacent to Lake Annie, Archbold Biological Station. Bees nested in the exposed sand of roadside or in the center region between the wheel ruts.



analyzed by principal components analysis. The log-transformed linear measurements were then regressed on the log-transformed scores (overall size) to calculate scaling coefficients in the equation: $Y=bX^a$. The null hypothesis of isometry is equal to an α of 1.0. The significance of the observed deviations of α from a slope of 1.0 were evaluated using a t-test (Sokal and Rohlf 1981).

Daily and Seasonal Activity.—Individual *Heterotheca* plants and *P. graenicheri* nests were monitored daily from ca 0800–1700 hrs, EST. Groups of composite flowers, or capitula, were observed for the presence of *P. graenicheri*, either as individuals or in copula, and for other insects. Nest entrances were covered with transparent plastic cups and were monitored for exiting or returning females in order to assess solitary/communal nesting behavior.

Bee specimens, collected on *Heterotheca* or in Malaise traps, from the Station collection were used to determine the seasonal occurrence of adults. Nests excavated in August and December also provided insights into the annual cycle of this species.

Nest Architecture.—Five nests were completely excavated from the surrounding substrate after blowing a fine mist of plaster of Paris powder into the entrances. Sand grains were removed with a teaspoon, pen-knife, or a #2 camel's hair paint brush. Additional substrate was removed from a 10 cm radius surrounding the main tunnel to locate plugged laterals.

Immature bees removed from excavated nests were either preserved in Kahle's solution for later dissection and description, or were placed in small wells in a covered plastic culture dish for laboratory rearing. Pollen balls still contained within open

cells were carefully wrapped in tissue paper and transported in cork-stopped vials.

Immature Stages.—Living bee larvae were maintained in culture for as long as possible in covered plastic dishes containing moist paper towels, and were then preserved in Kahle's solution upon death. No adults were reared. Specimens were ultimately transferred to alcohol or freeze dried for examination by light or scanning electron microscopy.

Mating Behavior.—Foraging females and males were observed throughout the day (0800–1700 hrs, EST) on capitula of *Heterotheca* and *Chrysopsis*. Unimpeded matings were timed to the nearest second. Only matings viewed from initiation of contact until uncoupling, with no obvious outside interference, were recorded.

RESULTS

Taxonomy.—Until recently *P. graenicheri* Timberlake was known only from the short type series and a pair of topotypes collected by S. Graenicher in southern Florida (Timberlake 1947, 1956; Mitchell 1960). Five male paratypes (USNM) exhibited little variation in color pattern, and the genae were either unarmed or possessed only a very small tubercle (Fig. 2B). A series of 75 males and 90 females collected at the Archbold Biological Station by Mark Deyrup and ourselves shows more variation in male coloration and morphology.

In the males the pair of small, lateral face marks above the clypeus are occasionally lacking, and the pronotum may sometimes have a pair of small yellow markings. The differences in coloration are not related to the comparative size. Males are 3.5–5.0 mm long, and the forewings are 2.5–3.3 mm long.

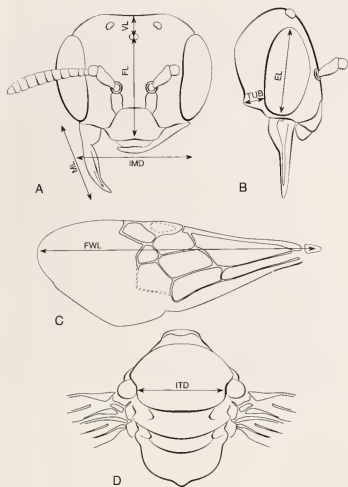


Fig. 2. A, Frontal view of head; B, lateral view of head; C, forewing; D, dorsal view of mesosoma. Eight linear measurements used in morphometric analysis are shown: VL = vertex length, FL = face length, IMD = intermandibular distance, ML = mandible length, EL = eye length, TUB = tubercle length, FWL = forewing length, ITD = intertergal distance.

Some females have the pair of transverse white markings on the fourth metasomal tergum reduced in size or lacking. The first tergum may be immaculate, but usually there is a pair of small lateral spots. Sometimes the first tergum may have an additional pair of small, central spots, and the four spots may be very narrowly separated from each other. Females are 4.5–5.2 mm long, and the forewings are 2.8–3.3 mm long.

Females key without difficulty to *P. graenicheri* in Timberlake's key to the subgenus *Hexaperdita* (1956). Larger males, however, may not key properly because the head is more subquadrate than rounded, and the gena has a large tubercle. There is no problem if one has an adequate series showing the allometric development of the head. But with a single large male, it may be necessary to extract the genitalia to separate it from *boltoniae* or *foveata*, to which it may key.

Neither sex keys properly in Mitchell (1960). Females will key to *graenicheri* (couplet 9) only if the markings on metasomal terga are changed from yellow to white. Only the smallest males, lacking both a tubercle on the gena and lateral face markings, key out at *graenicheri* (couplet 20). More small males would key out properly if the couplet were modified to indicate that lateral face markings usually are present though small. Males with a tubercle on the gena do not key correctly because Mitchell used presence or absence of a tubercle or spine in his first couplet to separate two groups of species, and *graenicheri* does not appear in the tuberculate group.

Morphometrics.— Table 1 presents the means and standard errors of the eight linear measurements. The regression analysis (Table 2) indicates significant deviation from isometry in six of the eight variables. The variables showing the strongest positive allometry are tubercle length (TUB), mandible length (ML), and vertex length (VL) (Fig. 3A,C,D). These trends reflect the fact that male head shape undergoes profound alterations with increased overall size (Fig. 4, A–F). Increased size results in disproportionate increase in tubercle length, mandible length, and expansion in the region of the head capsule dorsal to the median ocellus (vertex length, VL). Elongation of the tubercle is, in part, a result of an increase in overall genal width with increased body size. Tubercle length, with a scaling coefficient of 6.0, shows extremely pronounced positive allometry. A scaling coefficient of this magnitude indicates that a 20% increase in overall size results in a 3-fold increase in tubercle length. Other variables, such as eye length (EL), face length (FL), and forewing length (FWL) increase in proportion to overall size.

Daily and Seasonal Activity.— Bees were present on capitula on sunny days between 1000 and 1630 hrs. Males were present ca 30 min prior to females. During the peak foraging time, ca 1100 to 1430 hrs, several bees of both sexes were frequently encountered on a capitulum. Mating was observed throughout the foraging period. Both males and females remained active during periods of strong breezes, heavy cloud cover, and light rain. Females were observed initiating new nests as late as 1630 hrs. All nests observed or excavated contained a single adult female ($n = 25$).

This species is seemingly univoltine with a protracted emergence period so that adults may be present for several months. Newly transformed, teneral adults still underground were collected

during August 1989 in addition to flying adults. No adults developed from larval bees brought to the lab, however bivoltinism cannot be totally ruled out. Specimens collected by Mark Deyrup in 1986 bear labels indicating adult activity during late July, September, October, and early November. Nests excavated during late December contained only diapausing prepupae.

Nest Entrances.—Nest entrance/exit holes were circular, ca 3 mm in diameter, and never in the center of the tumulus. Radial tumuli were formed of loose sand grains pushed from the nest during a female's nest excavation. Each nest had only a single entrance. Entrances were closed with sand grains when a female was inside and remained open while she was away. Infrequently, a nest remained open while the female was inside, but nests were always closed at night.

Emergence holes (lacking tumuli) were numerous throughout the site, while entrances were more

Table 1. Means and standard errors of linear measurements, in mm ($n = 41$). See Figure 2 for measurements (TUB = tubercle length; EL = eye length; ML = mandible length; VL = vertex length; FL = face length; IMD = intermandibular length; ITD = intertegular length; FWL = forewing length).

TUB	0.17 ± 0.01
EL	0.69 ± 0.01
ML	0.67 ± 0.02
VL	0.10 ± 0.002
FL	0.87 ± 0.01
IMD	0.77 ± 0.01
ITD	0.85 ± 0.01
FWL	2.89 ± 0.03

dispersed and loosely aggregated. One entrance studied had an arrangement of small twigs encircling the opening. Upon displacement of the twigs to a location ca 6 cm away, the returning female flew directly to the center of the twigs instead of to her nest. This action was repeated for ca 8 min

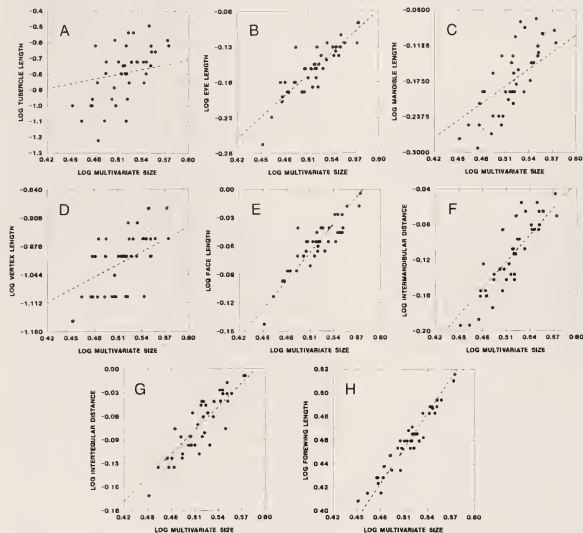


Fig. 3. A-H. Relationships between eight linear measurements and overall body size (data log-transformed) for 41 male *Perdita graenicheri*. Solid line indicates reduced major axis regression line and dashed line indicates null hypothesis of isometry (slope = 1.0). See Table 2 for major axis regression equations.

Table 2. Reduced major axis regression equations for eight linear measurements regressed on overall size. See Figure 2 for measurements (TUB = tubercle length; EL = eye length; ML = mandible length; VL = vertex length; FL = face length; IMD = intermandibular length; ITD = intertegular length; FWL = forewing length).

TUB = 1.26×10^{-4} (SIZE) ^{0.60}	t = 6.65*** $s_a = 0.751$
EL = 0.18 (SIZE) ^{1.14}	t = 1.58 ns $s_a = 0.089$
ML = 0.058 (SIZE) ^{2.14}	t = 5.14*** $s_a = 0.211$
VL = 6.4×10^{-3} (SIZE) ^{2.28}	t = 4.49*** $s_a = 0.286$
FL = 0.29 (SIZE) ^{0.94}	t = 1.02 ns $s_a = 0.286$
IMD = 0.15 (SIZE) ^{1.37}	t = 3.68*** $s_a = 0.101$
ITD = 0.18 (SIZE) ^{1.30}	t = 3.05** $s_a = 0.097$
FWL = 0.98 (SIZE) ^{0.90}	t = 2.68* $s_a = 0.036$

before the bee finally located her nest entrance.

Burrows.—Nests consisted of a primary unlined shaft ca 3 mm in diameter, and a series of shorter unlined lateral shafts each of which ended in a single cell. Initially main burrows descended at an angle of ca 15° for distances of 2 to 7 cm. Then the main burrows turned abruptly downward, descending vertically for 23 to 42.5 cm. Lateral shafts were perpendicular to the main shaft and branched off of it at depths of 22 to 34 cm. They radiated in various directions horizontally from the main shaft and were 2 to 5 cm in length.

Laterals containing completed cells were filled with sand. The main burrow of one excavated nest had been filled with sand from 7 to 14 cm in depth.

Cells.—Cells were formed at the ends of laterals by enlargement of the tunnels to a diameter of ca 3.5 mm. Cells were ca 4 mm in length and sloped slightly downward toward the rear. A single cell was constructed at the end of the open lateral, provisioned, supplied with an egg, and then closed before another lateral and cell were excavated. The youngest cells were those deepest in the ground. Nests contained two to six cells, but because nest-

ing had been initiated only recently it is likely that nests excavated later in the season would contain a greater number of cells.

Upon first observing cells, they appeared to consist of unlined, non-manipulated sand grains. A drop of water placed in a cell was retained for several seconds, then flowed through. But cells gently removed from the substrate retained their shape and appeared to have a shiny, oily coating on the sand grains. Microscopic examination (light and SEM) of cells revealed a thin layer of a viscous material resembling nectar that bound the sand grains weakly to one another (Fig. 5A,C,D). The material did not have a sweet taste, was soluble in water after several seconds, and had a low melting point. Cell closures were indistinguishable from the sand grains plugging the laterals. However, all sand grains surrounding the pollen ball appeared to be impregnated by the cell binding material.

Provisions.—Pollen balls were perfect spheres consisting only of pollen of *Heterotheca subaxillaris* and nectar of *H. subaxillaris* or *Chrysopsis microcephala*. They were 2-2.5 mm in diameter, firm, and moist throughout. Completed balls were positioned in the rear of the cell and completely encased by a thin, presumably glandular, transparent coating (Fig. 5A,B). Like cell linings, pollen ball coatings initially repelled water, but became soluble within minutes, and dissolved in it.

Collected pollen was initially applied dry to trochanters, femora, and tibiae of the hind legs. As additional pollen was accumulated, pollen moistened with nectar was placed on top creating especially large bulges over the hindtibiae. Pollen brought into cells was deposited in the center and was not formed into a ball until the total provision was present. This pollen mass was slightly moist, but of a drier consistency than that of completed provisions, suggesting that additional nectar may have been added during formation of the ball.

Within the cells, both newly deposited pollen masses and completed pollen balls exhibited a very strong cheesy odor. Pollen on the legs of returning females did not have this odor, and pollen balls allowed to dry completely did not retain it. The odor, however, was so strong within the nest that the presence of a cell could be smelled before it was excavated from the plugged lateral. In fact, several undetected laterals were located by sniffing the substrate adjacent to the main shaft. Rozen (1967) noted that fermentation odors were not known from other panurgine nests.

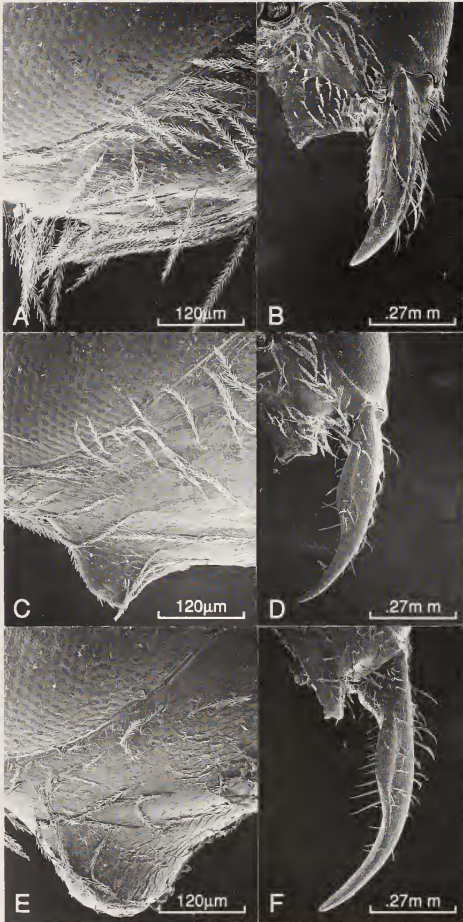


Fig. 4, A-F. Scanning electron micrographs of male *Perdita graenicheri* showing the left genal region (X250) and left mandible (X110). A and B show tubercle absent and short mandible. C and D show moderate tubercle and mandible. E and F show large tubercle and long mandible. Greater pubescence was noted for specimens lacking or with small tubercles.

Immature Stages.—Eggs were attached by their narrowed posterior ends to the top and rear of the pollen ball, farthest from the cell closure. Immature larvae were positioned upon their provisions while feeding, then rolled onto their dorsal surfaces prior to defecation. Prepupae rested in a curled U-shaped position on their large dorsal tubercles (Fig. 6A,B) with heads facing toward the cell closure. Fecal material consisted of a single string of pollen exines held on the venter until pupation, and remained with the exuvium. Quiescent, diapausing, post-defecating larvae demonstrated slow curling and uncurling movements. Indeed, wear to spines on the dorsal tubercles (Fig. 6C) was apparent in prepupae, but was not found in immature larvae. Cocoons were not present, but the prepupal integument was coated by a water-repelling secretion. This secretion (Fig. 6D) was relatively thick (ca 0.4 μ), unevenly distributed apparently due to several layers being secreted, and caused particles of debris to adhere to the larval cuticle.

Mating Behavior.—Males of *P. graenicheri* were never observed in or around nests. They were, however, numerous on and flying between the capitula of *Heterotheca* and *Chrysopsis*. Mating frequently occurred on the flower heads, while females gathered pollen. As noted for *P. texana* (Barrows et al. 1976), mating in *P. graenicheri* also was initiated prior to, during, or after all stages of pollen-nectar collection.

Males in most instances first landed next to females on capitula and then abruptly pounced on them. No apparent copulatory displays were observed, and males sometimes mounted pairs already in copula. Females were grasped from above, with the male initially holding her metasoma with his legs and her folded wings with his mandibles. Several seconds after initiating mating, however, males released their grasp, while remaining in copula, and either rested on the female's dorsum or at an angle of about 45° just above her. One female was observed actively grooming her metasoma throughout most of the copulation with apparent disregard of the male resting above.

Females of *P. graenicheri* seldom resisted copulation, but breezy conditions and the constant movement of swaying plants frequently resulted in foiled attempts to mate, as one or both bees were whisked away. We observed some females raising and lowering their metasomas as they walked across flower heads, which may indicate receptivity. Matings were of relatively long duration. Timed from initial union until an undisturbed separation

occurred, they ranged from 5 min 27 s to 12 min 20 s ($n = 10$, mean = 7 min).

Patrolling males flew rapidly between capitula, following a horizontal, zigzag flight pattern when above flower heads, and then descending quickly in a zigzag pattern if a female was present. Two or three males frequently were present hovering over a capitulum and often landed to take nectar. Males displayed little aggression towards one another, other than occasional bumping. This bumping motion consisted of one male pushing his head, as he crawled or while in flight, into the metasoma of another male. Bumping was most often directed towards a copulating male. These apparent attempts to dislodge males in copula were seldom successful, and usually resulted in the mating pair moving to another part of the capitulum, beneath the flower head, or to an adjacent capitulum. One pair, observed during a union of 7 min 5 s, was bumped three times by two different males. At one point the male in copula reared back to almost 180°, but did not become disengaged, and quickly resumed his original orientation.

Pairs separated as abruptly as they had coupled with no obvious post-copulatory behavior. Following copulation, males either paused momentarily, and then flew to another capitulum, or obtained nectar for 4-10 s ($n=25$) before leaving the flower head. Females occasionally flew to adjacent flower heads, but more often resumed pollen or nectar collection on the same blossom. In contrast to the single matings reported for *P. opuntiae* (Bennett and Breed 1985), *P. graenicheri* demonstrated multiple matings. Two females were observed mating within 30 seconds of a previous mating on the same capitulum.

Plant Associations.—Both male and female *P. graenicheri* visited the abundant flowers of two species of golden aster. Pressed plant specimens were identified as *Heterotheca subaxillaris* (Lam.) Britton & Rusby and *Chrysopsis microcephala* (Small) Shinners. While both plants were common in the study site, *Perdita* were seen most frequently on *H. subaxillaris*. Mating pairs and pollen collecting were observed only on *Heterotheca*. *Chrysopsis* was visited for nectar, and the literature, while giving no pollen source, also records the bees as visiting flowers of *Chrysopsis tracyi* (Graenicher 1930). Major reviews (Rickett 1967, Radford et al. 1968, Long & Lakela 1971) indicate that species currently placed in *Chrysopsis* Ell., *Hererotheca* Cassini, and *Pityopsis* Nutt. should be included in a single genus, *Heterotheca*.

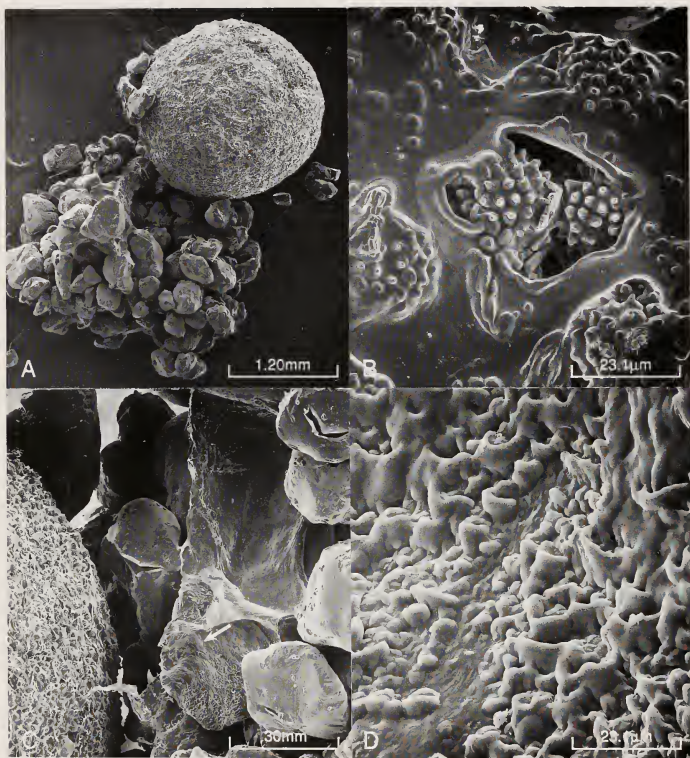


Fig. 5. Scanning electron micrographs from a *Perdita graenicheri* nest. A, Pollen ball showing water-repelling coating and several adherent sand grains (X25). B, Close-up of pollen ball showing *Heterotheca subaxillaris* pollen and a hole in the water-repelling coating (X1,030). C, Margin of pollen ball and adjoining sand grains with binding/water-repelling material (X100). D, Close-up of water-repelling material in sand grains (from region indicated in C.) (X1,030).

Associated Insects.— Two species of parasites, within the size range needed to enter *P. graenicheri* nests, were recorded at the nest site.

A female mutillid wasp, *Pseudomethoca torrida* Krombein, was collected near a number of *Perdita graenicheri* nest entrances. No other solitary bees were nesting in this circumscribed area, so it is possible that *torrida* is a parasitoid of this bee.

Danforth (1991b) found that *Pseudomethoca perditrix* Krombein parasitized post-defecating larvae of *Perdita portalis* Timberlake in New Mexico. This makes the association of *torrida* with *graenicheri* more probable. However, the closest relative of *torrida* is *frigida* (Smith), which is known only from halictine bee hosts.

Females of a small, cleptoparasitic halictid bee,

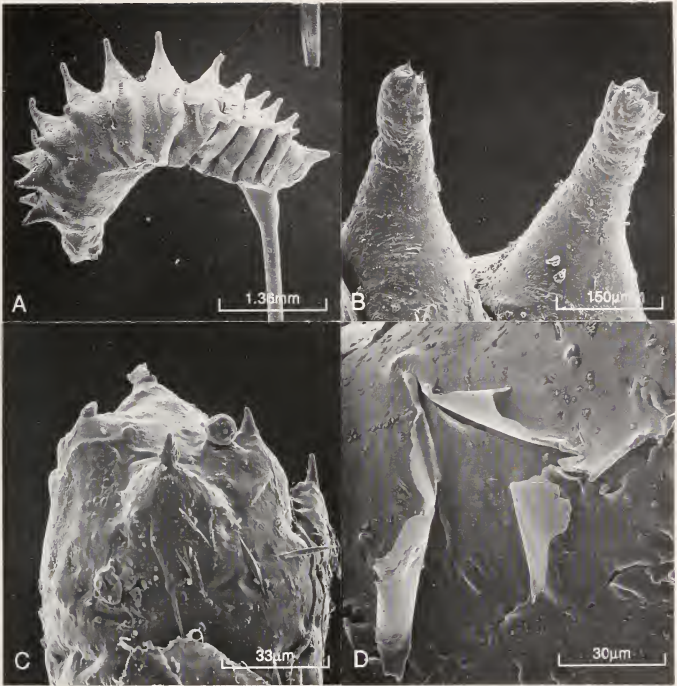


Fig. 6. Scanning electron micrographs of *Perdita graenicheri* prepupa. A, Entire prepupa showing large dorsal tubercles (X22). B, Tubercles are sclerotized and bear spines on their tips (X200). C, Close-up of tubercle showing debris adhering to the water-repelling secretion, and the wear to upper left spine (X900). D, Close-up of mid-region of a dorsal tubercle where the water-repelling secretion was cracked and peeling (X1,000).

Sphecodes sp., were noted inspecting nest entrances of *P. graenicheri* on two days, but none was captured. This species is a probable cleptoparasite of *P. graenicheri*.

Seven females and one male of a slender, delicate asilid fly, 3.0 to 3.5 mm long, were collected on the sand near nest entrances of *P. graenicheri*. They were not seen elsewhere on the surface of the sand, and were not observed entering bee nests. F.C. Thompson identified them as an undescribed species of *Townsendia* Williston. He believed that adults were not predaceous on the larger, rela-

tively stocky *P. graenicheri*, but suggested that their soil-dwelling larvae might prey upon the bee larvae.

Table 3 lists other species of Hymenoptera and Diptera collected on flowers of *Heterotheca* during the course of our study. All bees may be potential pollinators of *Heterotheca*. Males of the bee-like *Tachytes distinctus* are also likely to be effective pollinators, since each has a dense coating of pollen on the thoracic sternum. The female bombyliids may also be capable of pollinating flowers of *Heterotheca*, since all of them had pollen grains on

Table 3. Species of Hymenoptera and Diptera collected on *Heterotheca* during the course of our study.

Hymenoptera

Tiphidae:

Myzinum c. carolinianum (Panzer) 2 females, 1 male

Scoliidae:

Campsomeris plumipes fossilana (Fabricius) 1 male

Vespidae:

Eumenes s. smithii Saussure, 1 male

Pachodynerus erynnis (Lepelletier) 1 female, 1 male

Larriidae:

Tachytes distinctus Smith 3 males

Nyssonidae:

Bicyrtes capnoptera (Handlirsch) 1 female, 1 male

Halictidae:

Augochloropsis metallica (Fabr.) 1 female

Halictus ligatus Say 7 females, 1 male

Dialictus nymphalis (Smith) 1 male

Dialictus tamiamensis Mitchell 1 female

Dialictus tarponensis Mitchell 2 females

Dialictus regularis (Robertson) 1 female

Megachilidae:

Megachile (Acentron) albitarsis Cresson 1 female

Diptera

Bombyliidae:

Systoechus solitus (Walker) 1 female

Geron senilis (Fabricius) 1 female, 10 males

Systropus angulatus (Karsch) 1 female, 4 males

Lepidophora lepidocera (Wiedemann) 1 male

Exoprosopa species 1 male

Syrphidae:

Copestylum mexicanum (Macquart) 1 male

the proboscides and foretarsi (N. Evenhuis, pers. comm.).

DISCUSSION

Taxonomy.— The study of specimens collected on *Heterotheca* and *Chrysopsis* in USNM and in the Archbold Biological Station collection convinces us that a revision of *Hexaperdita* is needed. In addition to the variation in color pattern and male morphology of *P. graenicheri*, we noted a greater degree of color variation in *P. georgica* Timberlake than recognized hitherto. Some specimens of the latter species also will not key out correctly in either Timberlake (1956) or Mitchell (1960).

Morphometrics and Mating Behavior.— One of the more striking characteristics of *P. graenicheri* is the extreme variation in male head size and shape. While males show considerable head shape change with increased size, female heads scale essentially isometrically with respect to overall body size. Larger males of *P. graenicheri* have disproportion-

ately long genal projections, mandibles, mandibular gape, and an expanded vertex. Larger males, however, suffer a "cost" associated with these allometric changes: disproportionately small wings. Such allometric tradeoffs have been observed between structures associated with fighting and with flying in several other insect groups, and are commonly interpreted as the result of sexual selection (Eberhard 1982, Thornhill and Alcock 1983, Crespi 1988).

Male head allometry is widespread among *Perdita* species in the subgenera *Macrotera* Smith, *Macroteropsis* Cockerell, *Cockerellula* Strand, *Pseudomacrotera* Timberlake, *Hexaperdita*, and among species in *Perdita* sensu stricto (e.g., *P. koebelei* Timberlake, *P. dentata* Timberlake [Timberlake 1964]), as well as other panurgine genera, such as *Psaenythia* Gerstaecker and *Arhyosage* Brèthes. *Perdita* (*Macrotera*) *texana* (Cresson) shows positive allometry in mandibular length and gape, and vertex length. Positive allometry in vertex length is related to a disproportionate expansion of the mandibular adductor muscles, which insert on the dorsal surface of the head capsule, with increased overall size. Therefore, all variables showing positive allometry can be traced to the mandibles, which are used by males in fighting, and in grasping females at the initiation of copulation (Danforth and Neff in press). Positive head allometry appears to be a precursor of male dimorphism in *P. (Macroteropsis) portalis* Timberlake (Danforth 1991c) and *P. (Macroteropsis) mellea* Timberlake (Rozen 1972). The flightless, large-headed males in *P. portalis* also have genal projections, which appear to perform a defensive role, protecting the membranous proboscis fossa and neck region from the mandibles of other males during fierce intraspecific battles that can end in the death of one combatant.

Head allometry in *P. graenicheri* may be related to mating behavior, but it is puzzling that *P. graenicheri* males show no obvious agonistic interactions on capitula. Males of other *Perdita* species with positive head allometry (e.g., *P. portalis* and *P. texana*), can typically be seen fighting while on flowers. Head size in *P. graenicheri* may function primarily in grasping females at the initiation of copulation, especially since females are, overall, larger than males and are quite capable of dislodging them. The 12 min 20 s (740 s) mating recorded for *P. graenicheri* is the lengthiest reported to date for any species of *Perdita*.

Nesting Biology.— This study presents the first detailed observations on the nesting biology of a member of the subgenus *Hexaperdita*. In terms of social behavior, *P. graenicheri* is similar to many species of *Perdita* sensu stricto, in which females nest solitarily. However, in a related species of *Hexaperdita*, *P. ignota* Cockerell, females nest communally, with up to 10 females per nest ($n=6$ nests excavated; Danforth 1991a). Communal nesting occurs in other *Perdita* subgenera (e.g., *Macrotera* Smith, *Macroteropsis* Ashmead, *Cockerellia* Ashmead), and this trait shows considerable inter- and intra-specific variation. For instance, *P. lingualis* Cockerell and *P. albipennis* Cresson, two closely related species of *Cockerellia*, differ in the number of females per nest; the former is communal with up to 20 females per nest, while the latter was found to be solitary (Michener 1963, Danforth 1989). The number of females sharing a nest may also vary intraspecifically, from females nesting singly to communal associations of more than 30 females per nest (Danforth 1989, Neff and Danforth 1992).

The nest architecture and provisions of *P. graenicheri* are, in general, similar to members of the *Perdita* subgenera *Perdita* and *Cockerellia*. As in *P. graenicheri*, members of these subgenera coat the pollen ball with a glandular secretion, while the cell walls are usually reported to lack a hydrophobic coating (Rozen 1967). The observation of a very weak, water-soluble cell coating in *P. graenicheri* raises the possibility that nectar is used to coat cells in other species. In contrast, species of the subgenera *Macrotera*, *Macroteropsis*, and *Macroterella* produce a glandular, hydrophobic cell lining but do not coat the pollen ball (Danforth 1991b, Neff and Danforth in press).

Perdita graenicheri makes uncharacteristically short lateral tunnels for *Perdita*. While laterals may extend away from the main tunnel for up to 10 cm in some species (e.g., *P. portalis*, Danforth 1991c), *P. (Perdita) luciae* Cockerell and *P. (Hexaperdita) ignota* are the only other *Perdita* known to construct cells in a tight cluster around the main tunnel (Danforth 1989, Danforth 1991a).

Immature stages.— Data on egg placement and larval feeding and development are similar to those for other *Perdita* species. Of note, however, is the wearing down of spines on the dorsal tubercles of prepupae. Rozen (1967) mentioned the role of dorsal tubercles in movement of panurgine larvae. Observations of *P. graenicheri* suggest that during larval movements the spines play a role in preventing abrasion of the cuticle by sand grains, and may

further assist in preventing fungal infections by keeping larvae out of direct contact with the substrate.

Plant associations.— *Hexaperdita* contains approximately 30 species that, like *P. graenicheri*, are oligolectic on various genera of Asteraceae, primarily the subfamily Astereae. Associations with composites is widespread in the monophyletic assemblage including *Hexaperdita* Timberlake, *Pentaperdita* Cockerell and Porter, *Cockerellia*, *Procockerellia* Timberlake, *Callomacrotera* Timberlake, *Allomacrotera* Timberlake, and the Octomaculata group of *Perdita* Smith, sensu stricto (Danforth 1991a).

Although *Chrysopsis microcephala* and *Heterotheca subaxillaris* are similar and perhaps congeneric (see above), foraging and mating behaviors of *P. graenicheri* indicated that the bees were recognizing two different plants. Inasmuch as *P. graenicheri* visits *C. microcephala* only for nectar, it would be interesting to discover whether other eastern *Heterotheca* would be visited and for what purpose. A comparison of *P. graenicheri* behaviors to those of western *Perdita* species that visit *Heterotheca* might also be revealing.

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The First Mesozoic Vespidae (Hymenoptera) from the Southern Hemisphere, Botswana

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Abstract.—The first Mesozoic vespid (Euparagiinae) from the southern hemisphere, *Curiosivespa orapa* sp. nov., is described from deposits of middle Cretaceous age from Botswana. New information on skeletal features and probable sexual dimorphism in the genus are provided. Its presence in the southern hemisphere suggests that the subfamily had a cosmopolitan distribution 90 million years ago, but conclusions on areas of origin of the subfamily and the family await better information, especially on austral fossils.

All of the known Mesozoic fossils of Vespidae were recently surveyed by Carpenter and Rasnitsyn (1990) and Wenzel (1990). They comprise 11 species in three genera, *Priorvespa* Carpenter and Rasnitsyn (Priorvespinae), *Curiosivespa* Rasnitsyn (Euparagiinae) and *Celliforma* Brown (Polistinae or Vespinae, based on a nest only). These fossils are all from the northern hemisphere: Mongolia, the Buryatskaya Republic and Chita Region in Russia, Kazakhstan, and Utah in the U.S.A. There are almost 50 sites which have yielded Cretaceous insects, of which only about six are in the southern hemisphere (Hennig 1981; Grimaldi and Maisey 1990), and most of the latter have scarcely been reported on, so our knowledge is still highly fragmentary. Darling and Sharkey (1990) tabulated all known Cretaceous Hymenoptera. Only 11 out of the total of 214 species listed are from the southern hemisphere.

Recent excavations at the site of the Orapa Mine, Botswana, have revealed numerous Mesozoic fossils, dated as of middle Cretaceous (Coniacian-Cenomanian) age (Rayner et al. 1991), about 90 million years before the present. They include about 3000 specimens of insects, some of which have been studied by McKay (1990, 1991), McKay and Rayner (1986), Rayner (1987), Rayner and Waters (1989, 1991) and Waters (1989a, b, 1990). These are either impressions with little or no organic matter remaining or coalified compressions. The Hymenoptera comprise some 3 % of the insects (Rayner et al. 1991). Amongst them is a compression of a specimen of *Curiosivespa* (Vespidae, Euparagiinae), of which both the part and most of the counterpart

are present. These were photographed under oblique incident light and also under vertical illumination (fibre-optic ring light) under crossed polarizing filters (using a Wild M400 photomicroscope), and drawn with the aid of a drawing tube using a Wild M8 stereo microscope. The specimen is in a reddish lamination no more than 1 mm thick. Attempts were made to expose the antennae and part of the right wing of the counterpart after it had been photographed. Although this was not entirely successful because of the soft fine-grained nature of the deposits and the extreme delicacy of the fossil, some additional information was obtained; this is included in the line figures and the descriptions.

CURIOSIVESPA Rasnitsyn 1975:113.

This genus now includes five species known from six specimens. The present specimen is only the second to include skeletal features. It is preserved in a different orientation from the other such specimen (No. 2783/261, Kazakhstan, sex undetermined; Carpenter and Rasnitsyn 1990: Fig. 2) and is a female. (The apparent differences in proportions of the flagellomeres and the appearance of the metasomal apex suggest to me that the Kazakhstan specimen is a male.) It provides information, which is probably of generic value, additional to that given by Carpenter and Rasnitsyn (1990). The following generic description is based on theirs, with changes and new information in *italics*; their paper and figures should be consulted for identification of wing veins and other features

labelled there. Features of the wings are illustrated in Figs. 5-8 and Carpenter and Rasnitsyn (1990: Fig. 1), skeletal features of the female in Figs. 1-8 and of the putative male in Carpenter and Rasnitsyn (1990: Fig. 2). Where I am uncertain about features because of indistinctness in preservation, I have used the word "apparently".

Description.— Body moderately slender; head, mesosoma and metasoma similar in width.

Head with ocellar triangle about equilateral; eyes long, fairly shallowly but angularly emarginate; gena in lateral view moderately wide dorsally, narrow ventrally. Antenna with scape elongate (nearly as long as distance between eyes at level of antennal sockets in female), pedicel somewhat elongate in male but short in female, flagellomeres very slender in male but apparently fairly stout and short in female; clypeus almost as long as wide, dorsal margin apparently very weakly concave and just below lower margin of antennal socket, apex apparently truncate; labrum exposed, almost semicircular, apparently well-sclerotized; antennal socket separated by about 1.2x its diameter from eye; preoccipital carina well-developed, complete dorsally, ending ventrally apparently near level of posterior margin of oral fossa, subocular furrow apparently present; oral fossa apparently broad, extending posteriorly about 0.6x distance to occipital foramen; mandible elongate, probably bidentate apically.

Mesosoma broadly longitudinally oval from above; mesoscutum almost as wide as long, about twice as wide and about 2.7x as long as scutellum; tegula small, apparently broadly oval; scutellum somewhat wider than long, almost oval but tending towards rectangular; metanotum a short posteriorly convex transverse band; propodeum short with posterolateral angles apparently smoothly rounded, anteriorly with a weak transverse carina merging with a median longitudinal carina. Mesopleuron with dorsal groove and lower part of scrobal furrow aligned, precoxal sulcus subparallel to this; metapleuron not constricted at endophragmal pit, lower part (*metepisternum*) well differentiated from upper part (*metepimeron*) and propodeum, with *metapleural sulcus* running anteroventrally from pit.

Fore wing as in *Euparagia* Cresson (first subdiscal cell strongly produced dorsoapically, third (second of Carpenter and Rasnitsyn) abscissa of CuA almost aligned with 1m-cu, first discal cell much longer than subbasal cell, first abscissa of M longer than RS+M, cu-a long and strongly to very weakly curved) except third submarginal cell at most subequal to second in length, not extending as far as apex of marginal cell, and 3rs-m smoothly curved instead

of strongly sinuous. Hind wing with crossvein rs-m strong, convex; free spurs of Rs and M distinct; cu-a straight, long, oblique, inserting on M+CuA shortly before divergence of M and CuA.

Legs fairly long and slender; mid and hind legs with basal tarsomere apparently at least twice as long as any subsequent tarsomere.

Metasoma moderately elongate; first segment probably longer than wide in male but slightly wider than long in female, not petiolate; no evident constriction between segments; female with six visible metasomal segments all similar in length, last segment simple and more or less conical; sting well-developed.

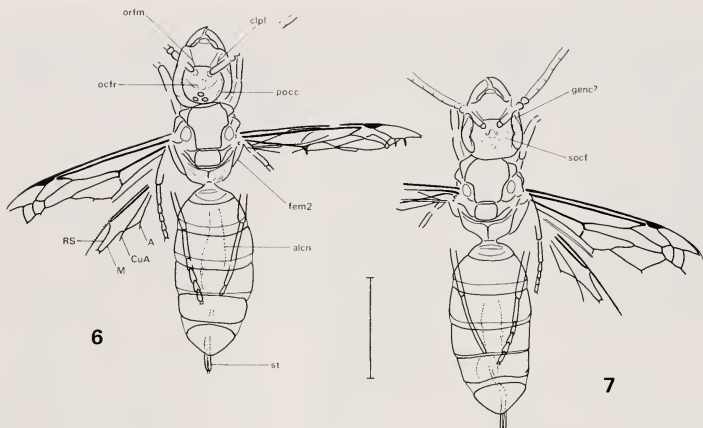
Curiosivespa orapa Brothers, new species

Figs. 1-8

Holotype female.— Size fairly small; fore wing length 10 mm, corrected body length about 13 mm (total length of specimen with head tilted, metasoma distended and sting protruded 17 mm). Metasoma apparently paler in color than head and mesosoma (pronotum and posterolateral areas on propodeum possibly paler also). Integument apparently without coarse sculpture. *Head:* Short genal carina apparently present ventrally; scape length 0.7x eye height, 0.8x distance between eyes at level of antennal sockets; pedicel very slightly wider than long, apparently about 0.5x as long as first flagellomere; first flagellomere length apparently about 0.25x eye height and about 2.0x width, second flagellomere apparently about 0.75x as long and as wide as first, next three flagellomeres each apparently about as long and as wide as second (very rough estimates since limits of flagellomeres very indistinct). *Wings:* Fore wing with pterostigma moderately long, about 3x length of prestigma; R₁ beyond this along wing margin except at extreme apex; second submarginal cell about as long as high, slightly longer than third submarginal, with basal angle almost 90° and at about mid-height of cell; third submarginal cell about 1.5x as high as long; 2m-cu received in second submarginal cell; third (second of Carpenter and Rasnitsyn) abscissa of CuA slightly shorter than 1m-cu; CuA₁ aligned with A at a very obtuse angle; cu-a almost straight, arising well beyond fork of M and CuA, first abscissa of CuA about half length of cu-a; free spur of A distinct. Hind wing with about 15 hamuli; free section of CuA apparently fairly long; fairly short free spur of A present. *Legs:* Mid femur about 0.6x as long as head width, as long as tibia and apparently about 2x as long as first tarsomere; first



Figs. 1-5. *Curiosivespa orapa*, holotype. 1, Part, vertical light, crossed polarizers. 2, Part, oblique incident light from top left. 3, Counterpart, vertical light, crossed polarizers. 4, Counterpart, oblique incident light from top left. 5, Part, left wing, vertical light, crossed polarizers. Scales: Figs. 1-4 = 5 mm; Fig. 5 = 2 mm.



Figs. 6-7. *Curiosivespa orapa*, holotype, left hind wing displaced to display venation. 6, Part (limits of tarsomeres approximate). 7, Counterpart (limits of antennomeres approximate). Scale = 5 mm. Abbreviations: A = anal vein; alcn = alimentary canal; clpl = lateral margin of clypeus; CuA = anterior cubital vein; fem2 = mid femur; genc = probable genal carina; M = medial vein; ocfr = occipital foramen; orfm = margin of oral fossa; pocc = postoccipital carina; RS = radial sector vein; socf = subocular furrow; st = sting.

tarsomere apparently about 0.6x as long as rest of tarsus, second to fifth tarsomeres apparently subequal. Hind first tarsomere apparently about 0.55x as long as rest of tarsus, second to fifth tarsomeres apparently subequal (very rough estimates since limits of tarsomeres very indistinct); hind arolium apparently well-developed. *Metasoma*: Apparently somewhat distended in holotype; first segment slightly wider than long, shallowly conical to campanulate; relative lengths of tergal sclerite apparently about 9:10:11:10:13.

Material examined.— Holotype: BOTSWANA: Orapa Mine, No. BP/2/27125/A (part) and BP/2/27125/B (counterpart), female; deposited in Bernard Price Institute of Palaeontology, University of the Witwatersrand, Johannesburg, South Africa.

Discussion.— This species keys to couplet 3 (*C. curiosa* Rasnitsyn and *C. magna* Rasnitsyn) in the key provided by Carpenter and Rasnitsyn (1990) but is easily distinguished from those species by the insertion of 2m-cu on the second submarginal cell (a condition like that in *C. derivata* Carpenter and

Rasnitsyn) and the almost straight cu-a. It is one of the smallest species, the same size as *C. curiosa*.

Curiosivespa differs from the only other known genus of Euparagiinae, *Euparagia*, in a number of ways. Thus, in *Curiosivespa* body size tends to be somewhat larger (body length more than 12 mm, but less than 9 mm in *Euparagia*; Bohart 1948), the clypeus and labrum are apparently less specialized (clypeus apicoventrally incised and labrum concealed in *Euparagia*), the antennae are relatively much more slender (especially in the male), the forewing has 3rs-m simplified (strongly sinuate in *Euparagia*), the hind wing has cu-a long and oblique (shorter and meeting CuA and A at about right angles in *Euparagia*) and the first metasomal segment is apparently less swollen posteriorly. There is strong evidence that the middle Cretaceous environmental conditions at Orapa were considerably moister and more vegetated than today: a temperate, seasonal, forested habitat with high humidity and close proximity to water is indicated (Rayner et al. 1991). These conditions are probably some-

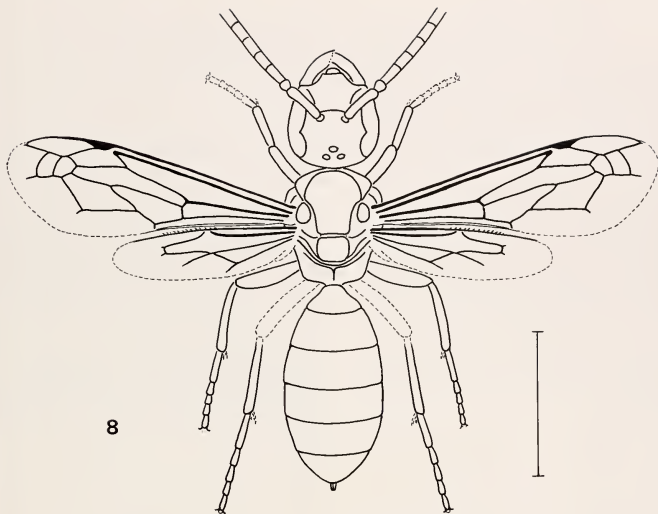


Fig. 8. *Curiosivespa orapa*, reconstruction, dorsal view, head tilted in anterior view (structures for which no information is available in holotype indicated by dashed lines). Scale = 5 mm.

what different from those appertaining in those areas where *Euparagia* occurs, namely the arid southwestern regions of the U.S.A. The two genera may thus also differ in their habitat requirements.

In his analysis of the relationships amongst the higher taxa of Vespidae, Carpenter (1981) postulated that the Euparagiinae had an austral origin on the basis of his cladogram. More recently, on the basis of the apparently exclusively boreal distribution of *Curiosivespa* and *Euparagia*, the only genera included in the subfamily, Carpenter changed his mind and stated that "the subfamily is of Laurasian origin" (Carpenter and Rasnitsyn 1990). The discovery of a specimen which is indubitably a species of *Curiosivespa* of appropriate age (although not as old as some of the Asian specimens) from the southern hemisphere at the very least indicates an early cosmopolitan distribution of the subfamily without any specification of place of origin. The dangers of giving excessive weight to the distribution of fossils in refuting conclusions suggested by cladograms based on modern taxa are thus well

demonstrated. The exclusively boreal distribution of Priorvespinae, the most basal subfamily which is known only from fossils (Carpenter and Rasnitsyn 1990), is suggestive of a boreal origin for the family, but any firm conclusions must await better information on austral fossils.

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Viruses and Virus-like Entities in the Parasitic Hymenoptera

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Abstract.— We provide here an overview of viruses and virus-like agents affecting the parasitic Hymenoptera. An amazingly complex variety of such agents is now known. By far the majority are non-pathogenic, replicating primarily in the female reproductive tract, from which they are often if not invariably delivered into host insects during oviposition; most, in fact, would appear to be beneficial to the parasitoids in which they are found. Emphasis is necessarily placed on the better known polydnnaviruses, which are carried by perhaps tens of thousands of braconid and ichneumonid species. Polydnnavirus DNA appears to be permanently integrated into parasitoid genomes, thereby ensuring transmission to all progeny; in keeping with this observation, these, where present, are known to be required for successful parasitism. Relationships among the polydnnaviruses are discussed in terms of their possible relevance to parasitoid phylogeny and classification.

Like other insects, the parasitic Hymenoptera must presumably from time to time be subject to infectious viral disease. There are, to be sure, numerous opportunities. For example, viruses could readily spread horizontally between larval cohorts of those species which are either gregarious or polyembryonic. The host itself could represent a source of infectious virus for developing parasitoid larvae, and possibly as well for adult wasps feeding upon hemolymph exuded from oviposition sites. Finally, infectious disease agents could be transmitted mechanically via contaminated ovipositors of hyperparasites. Yet, oddly enough, viral diseases in the parasitic Hymenoptera are seemingly rare. Reasons for this are not immediately evident. Conceivably, many parasitoids succumb to disease prior to emergence from their hosts; such events might easily go undetected, even in a laboratory situation.

A SURVEY

In fact, we are aware of only one example of a recognized viral pathogen of parasitoids: a recently described baculovirus from the braconid, *Microplitis croceipes* (Cresson) (Hamm et al. 1988); thus far, replication has been observed only in fat body tissue. A baculovirus has also been described from the ichneumonid parasitoid, *Mesoleius tenthredinis* (Morley) (Stoltz et al. 1981). Like most of the viruses and virus-like agents that are de-

scribed below, this virus appears to replicate only in the female reproductive tract and/or its accessory glands; like all of the agents described below, the *Mesoleius* baculovirus is apparently non-pathogenic (at least for the parasitoid host).

The best-known of the parasitoid-associated viruses are the polydnnaviruses, which now constitute a recognized virus family (Polydnnaviridae) within which 2 groups are recognized, namely the bracoviruses and ichnoviruses, which differ in terms of both morphology and host range; the polydnnaviruses will be subsequently examined in considerable depth, and so are not discussed further here. Emerging as potentially a second virus family is a growing assemblage of entities having as a distinct common morphology a long, filamentous, enveloped nucleocapsid. Examples of these viruses are known from both braconid (Stoltz and Vinson 1977 and 1979a; Styer et al. 1987; Hamm et al. 1990;) and ichneumonid (Krell 1987) parasitoids; one has been shown to replicate in host tissues (Styer et al. 1987). In terms of nucleocapsid morphology, the filamentous virus observed in the braconid *Cotesia congregata* (Say) (Stoltz and Vinson 1977, 1979a) very closely resembles a filamentous virus from the tsetse fly *Glossina pallidipes* Austen (Odindo et al. 1986). It should be noted that a somewhat similar virus has been described from honey bees (Clark 1978; Bailey et al. 1981).

A variety of other viruses (again all non-pathogenic) have been reported from parasitoid species (Table 1). Stoltz et al. (1988a) describe an unusual virus (designated CmV2) which apparently replicates in all individuals of certain *Cotesia*

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Table 1. Viruses and virus-like particles in the parasitic Hymenoptera.

Type	Host species	Site(s) of replication in:		References
		parasitoid	host	
Viruses				
baculovirus	<i>Mesoleius tenthredinis</i>	ovary	not known	Stoltz (1981)
baculovirus ¹	<i>Microplitis croceipes</i>	fat body	not known	Hamm et al. (1988)
rhabdovirus	<i>Diachasmimorpha longicaudatus</i>	venom gland	not known	Lawrence and Akin (1990)
poxvirus	<i>Diachasmimorpha longicaudatus</i>	venom gland	hemocytes	Lawrence and Akin (1990)
long, filamentous (unclassified)	<i>M. croceipes</i> <i>Cotesia congregata</i> <i>Cotesia hyphantriae</i> <i>Diadegma terebrans</i>	ovary	not known	Stoltz and Vinson (1977, 1979a) Krell (1987), Hamm et al. (1990)
unclassified	<i>Cotesia melanoscela</i>	ovary, muscle, hemocytes, tracheal epithelium	fat body, hemocytes	Stoltz et al. (1988a)
polydnavirus	see Table 2	ovary	no	Stoltz and Vinson (1979a) Stoltz et al. (1981) Krell (1991)
Virus-like particles ²				
	<i>Venturia canescens</i>	ovary	not known	Rotheram (1967, 1973) Feddersen and Schmidt (1986)
	<i>Meteorus leviventris</i>	venom gland	not known	Edson et al. (1982)
	<i>Bathyplectes</i> spp.	ovary	not known	Hess et al. (1980), Stoltz et al. (1981)
	<i>Leptopilina heterotoma</i>	"long gland" ³	not known	Rizki and Rizki (1990)

¹ The only viral pathogen known thus far in the parasitic Hymenoptera.

² So-called either because they do not contain nucleic acid (e.g., *Venturia*), or else because they bear no resemblance to any known viruses.

³ Convincing evidence for particle morphogenesis has yet to be provided.

melanoscela (Ratzeburg) populations. Having large fusiform nucleocapsids, this virus superficially resembles the ichnoviruses (Stoltz and Faulkner 1978), ascoviruses (Federici 1983), and a virus-like particle observed in fire ants (Avery et al. 1977); however, unlike any of the polydnaviruses, CmV2 does not have a segmented genome (Stoltz et al. 1988a). Replicating in the ovarian calyx, among other tissues, CmV2 is able to gain entry into the oviduct, and is subsequently injected into host larvae during oviposition; replication ensues, but apparently with no ill effect.

Lawrence and Akin (1990) have recently described two "virus-like" agents replicating in the venom apparatus of the braconid, *Diachasmimorpha longicaudatus* (Ashmead). One of these is almost

certainly a rhabdovirus, and the other an entomopoxvirus. Both are apparently delivered to host animals during oviposition, with subsequent replication occurring in the case of at least one of them (the poxvirus). It now seems probable that both viruses are present in *all* individuals (Lawrence, personal communication). No information is yet available concerning the effects, if any, of either virus upon host physiology. Virus-like particles have also been described in the venom apparatus of another braconid, *Meteorus leviventris* (Wesmael) (Edson et al. 1982) but these remain uncharacterized.

Recently, a particulate secretion has been reported by Rizki and Rizki (1990) in the cynipoid wasp *Leptopilina heterotoma* (Thomson). These

particles, which are apparently formed within an accessory gland of the wasp ovary, are immunosuppressive within host *Drosophila* larvae. Specifically, the *Leptopilina* particles can be shown to destroy lamellocytes, which are otherwise capable of encapsulating parasitoid eggs (Rizki and Rizki 1984). At this point, it is not known whether the particles contain nucleic acid, and details of morphogenesis are unavailable. Accordingly, these particles are best referred to as "virus-like". Since the particles can be readily purified, it seems likely that additional information relating to this fascinating biological system will emerge in the near future.

Finally, much of the inspiration leading to the discovery and characterization of the polydnaviruses (see below) has surely been derived from the early studies of Salt and Rotheram on the ichneumonid parasitoid, *Venturia canescens* (Gravenhorst) and its host *Anagasta kuhniella* (Zeller); for details, the reader should consult reviews by Salt (1968, 1970). Briefly, Rotheram (1967) identified a particulate secretion comprised largely of virus-like particles produced in the nuclei of cells found in the calyx, a region of the ovary situated between the ovarioles and the oviducts. Salt (1968, 1970), and more recently, Feddersen and Schmidt (1986), showed that "calyx fluid" conferred resistance on parasitoid eggs to host immune responses. It has now been determined that the virus-like particles share antigenic determinants with one or more host proteins (Feddersen and Schmidt 1986), suggesting that the parasitoid egg surface (which is coated with particles; Rotheram 1973) is recognized as self, hence evading surveillance by the host immune system. Despite their origin in cell nuclei, *Venturia* particles do not contain DNA (Feddersen and Schmidt 1986). A reasonable working hypothesis might posit that *Venturia* carries a "defective" polydnavirus, the genome of which resides within the parasitoid genome, but fails to become packaged into virus particles.

THE POLYDNAVIRUSES

In what follows, we provide a brief overview of what is currently known about the polydnaviruses. In so doing, we will highlight those features which distinguish this group from what may be referred to as "typical" viruses. Finally, considerable emphasis will be placed on the question of why

polydnaviruses should be of interest to the hymenopterist community.

Classification.—With regard to viruses replicating in animal hosts, the great majority may be conveniently assigned to a particular family on the basis of three criteria: site of replication (nucleus vs. cytoplasm), morphology, and information concerning the nature of the genome. In the case of the polydnaviruses, the latter has particular significance as a diagnostic tool, since it allows us to readily distinguish these viruses from all others. Briefly, encapsidated polydnavirus genomes consist of a *polydisperse* population of double-stranded circular DNA molecules (hence, *polydnavirus*; Stoltz et al., 1984); within this population, there exist at least 20-30 classes of molecules differing in terms of molecular size (Krell and Stoltz 1979, 1980, Stoltz et al. 1981, Krell et al. 1982). As will be seen (see: Life Cycle, below), there also exists a linear, chromosomal, copy of the polydnavirus genome. In terms of morphology, the polydnaviruses comprise two quite distinct groups, the so-called bracoviruses and ichnoviruses; as the names suggest, these are found, respectively, in certain braconid and ichneumonid wasps only. Bracovirus particles consist of cylindrical nucleocapsids, of variable length, surrounded either individually or in groups by a single unit membrane; ichnovirus particles consist of fusiform nucleocapsids surrounded by two unit membrane envelopes (Stoltz and Vinson 1979a). Typical examples are given in Figure 1. Bracovirus structure clearly resembles that of the baculoviruses, at least in some respects (Stoltz and Vinson 1979a); ichnovirus particles only superficially resemble a number of large viruses having lenticular nucleocapsids (e.g. Avery et al. 1977; Stoltz and Faulkner 1978; Federici 1983).

Distribution.—Preliminary lists of species carrying polydnaviruses have been provided by Stoltz and Vinson (1979a) and Stoltz et al. (1981); more recent compilations are given by Krell (1991) and in Table 2. Among the Braconidae, polydnaviruses are known from three subfamilies: Cheloniinae, Microgastrinae, and Cardiochilinae. Within the same lineage are included several other subfamilies (Miracinae, Khoikhoiinae, Adeliinae and probably also Neoneurinae; see Fig. 2), some or all of which might reasonably be predicted to carry polydnaviruses. Ichnoviruses have been, thus far, detected primarily in the Campopleginae. However, isolates from *Glypta* spp. (Stoltz et al. 1981,

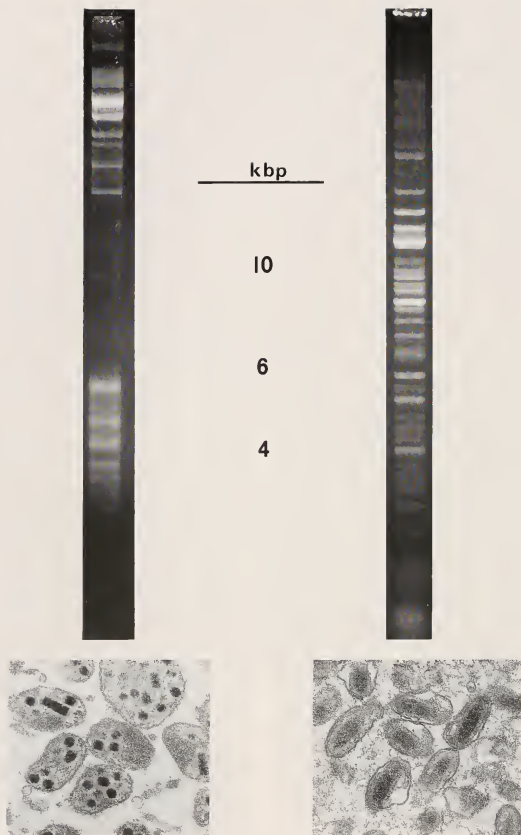


Fig. 1. Typical examples of polydnavirus particles and encapsidated genomes. Below left is shown an electron micrograph of a bracovirus (from *Protopanteles paleacritae*) and, to the right, an ichnovirus (from *Hyposoter exiguae*). Above these, 0.8% agarose gel electrophoretic profiles of DNAs extracted from calyx fluids are seen after ethidium bromide staining; approx. 1 μ g of viral DNA is present in each lane. Left, bracovirus DNA from *Microplitis croceipes*; right, ichnovirus DNA from *H. rivalis*. The bands represent different populations of intact (i.e., undigested) circular DNA molecules. Size markers (in kilobase pairs) are given for the superhelical forms of viral genome segments. Experience thus far suggests that bracovirus genome segments typically exhibit a relaxed open circular topology, and are for the most part larger than 10 kb. Ichnovirus genome segments are often smaller (e.g., 2-10 kb in the genus *Hyposoter*); superhelical forms tend to predominate, especially when DNAs have been extracted from purified virus particles.

Table 2. Parasitoid species in which polydnaviruses have been found. For references, consult Stoltz and Vinson (1979a), Stoltz et al. (1981), and Krell (1991). Ichnoviruses were not, prior to the present report, known from either *Dusona*, *Lissonota* or *Synetaeris*. *M. demolitor* is also a new listing (see Strand and Dover 1991).

BRACONIDAE

Cheloninae

- Ascogaster argentifrons* (Provancher)
- Ascogaster quadridentata* Wesmael
- Chelonus blackburni* Cameron
- Chelonus altitudinis* Viereck
- Chelonus nr. curvamaculatus* Cameron
- Chelonus insularis* Cresson
- Phanerotoma flavitestacea* Fischer
- Campoletis sonorensis* (Cameron)

Cardiochilinae

- Cardiochiles nigriceps* Viereck

Microgastrinae

- Apanteles crassicornis* (Provancher)
- Apanteles fumiferanae* Viereck
- Cotesia congregata* (Say)
- Cotesia flavipes* (Cameron)
- Cotesia glomerata* (Linnaeus)
- Cotesia hyphantriae* (Riley)
- Cotesia kariyai* Watanabe
- Cotesia marginiventris* (Cresson)
- Cotesia melanoscela* (Ratzeburg)
- Cotesia rubecula* (Marshall)
- Cotesia schaeferi* (Marshall)
- Diolcogaster facetosa* (Weed)
- Glyptapanteles flavicoxis* (Marshall)
- Glyptapanteles indiensis* (Marshall)
- Glyptapanteles liparidis* (Bouché)
- Hypomicrogaster eddytolophae* (Muesebeck)
- Microgaster canadensis* Muesebeck

- Microplitis croceipes* (Cresson)
- Microplitis demolitor* Wilkinson
- Pholetos ornigis* (Weed)
- Protapanteles paleacritae* (Riley)

ICHNEUMONIDAE

Banchinae

- Glypta fumiferanae*
- Glypta* sp.
- Lissonota* sp

Campopleginae

- Campoletis aprilis* (Viereck)
- Campoletis flavicincta* (Ashmead)
- Campoletis* sp.
- Casinaria forcipata* Walley
- Casinaria infesta* (Cresson)
- Casinaria* sp.
- Diadegma acronycta* (Ashmead)
- Diadegma interruptum* (Holmgren)
- Dusona* sp.
- Eriborus terebrans* (Gravenhorst)
- Hyposoter annulipes* (Cresson)
- Hyposoter exiguae* (Viereck)
- Hyposoter fugitivus* (Say)
- Hyposoter lymantriae* (Cushman)
- Hyposoter rivalis* (Cresson)
- Olesicampe benefactor* Hinz
- Olesicampe geniculatae* Quednau & Lim
- Synetaeris tenuifemur* (Walley)
- Tranosema* sp.

and unpublished data) are known; this genus is included in a different taxon: Banchinae (Gauld 1984; Wahl 1988). The two subfamilies are fairly closely related, so that surveys of additional related subfamilies (Figure 3) for the presence of polydnaviruses would be worthwhile.

Preliminary observations suggest the following:

- each "affected" parasitoid species carries a different polydnavirus characteristic of that species.
- if one species within a particular genus carries polydnavirus, they all are likely to.

Needless to say, most groups of parasitic Hymenoptera have not yet been examined in any systematic way for the presence of polydnaviruses. Incidental observations, however, suggest that these viruses are not present in *Alysia* (Alysiinae), *Bracon* (Braconinae), or *Aleiodes* (Rogadinae) in the Braconidae (Stoltz, unpublished). Although both

Alysia and *Aleiodes* are endoparasitic, they appear to comprise a lineage independent from the microgastrine complex of subfamilies (Tobias 1967; Capek 1970; Shaw 1983; Gauld 1988; Gauld and Bolton 1988; Quicke and van Achterberg 1990; Whitfield in press). Among the ichneumonid taxa, again little is known concerning the incidence of polydnavirus carriage, if any, within the majority of subfamilies.

Life Cycle.—Polydnavirus replication is strictly nuclear, and appears to be limited to the ovarian calyx of certain species of parasitic Hymenoptera. Replication begins during the pupal stage (Norton and Vinson 1983; Theilmann and Summers 1986), and has long been assumed to be triggered by hormonal changes occurring during morphogenesis of the ovary; more recently, viral replication in explanted *Campoletis sonorensis* (Cameron) ovaries has been shown to be induced by ecdysone (Webb and Summers in press). Aside from this observation, the molecular details of viral replication remain

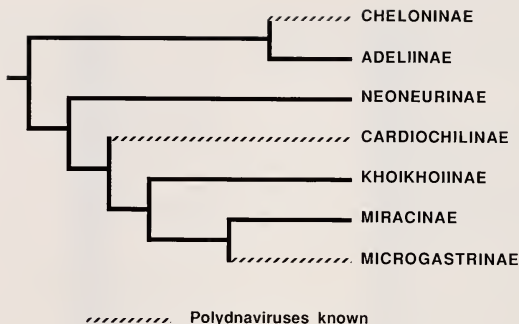


Fig. 2. Phylogenetic hypothesis for the subfamilies of Braconidae that carry polydnaviruses. Adapted from Austin (1990); based also on data from Mason (1983). There is no general agreement that the Ichneutinae also belong in this complex (see, e.g., Quicke and van Achterberg 1990), but the possibility exists.

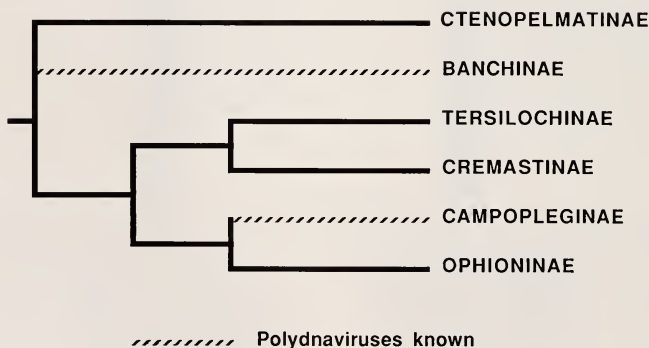


Fig. 3. Phylogenetic hypothesis for the subfamilies of Ichneumonidae that carry polydnaviruses. Adapted from Gauld (1985); the Anomaloninae probably also belong here (Wahl 1988).

obscure. Following replication, mature particles enter the lumen of the reproductive tract where they comprise, as seen previously with *Venturia*, a so-called "calyx fluid". The oviducts, then, contain both eggs and virus; it should therefore come as no surprise to learn that both are injected into host animals during oviposition (Stoltz and Vinson 1977, 1979b). Extensive electron microscopic studies carried out in the mid to late 1970s established that:

1) polydnavirus replication occurs in the ovaries of *all* females of *all* affected species, and 2) polydnaviruses are "designed" for export (i.e., to the parasitized host). Each of these observations has far-reaching implications. The first indicates that polydnavirus transmission within parasitoid populations occurs with 100% efficiency, suggesting further that polydnaviruses must have an important role to play in the parasitoid life cycle.

The second observation suggests that **a functional role for polydnavirus particles should be sought in the host.**

We may think of polydnavirus "transmission", and indeed the polydnavirus life cycle itself, as consisting of two pathways (Stoltz in press). In one, polydnavirus DNA is transmitted within *parasitoid* populations; in the other, polydnavirus particles are transmitted to *host* insects during oviposition, the consequences of which will be discussed below. These two pathways are considered here in the order given, recognizing however that they are mutually interdependent. Within parasitoid populations, polydnaviruses are transmitted genetically in the form of proviruses. This conclusion is based upon two lines of evidence. First, genetic crossing experiments have clearly demonstrated that both ichnovirus and bracovirus genome segments are transmitted to parasitoid progeny according to simple Mendelian rules (Stoltz 1990). Secondly, linear DNA sequences cognate to polydnavirus genome segments are covalently linked to parasitoid chromosomal DNA; this, too, has been shown for both ichnoviruses (Fleming and Summers 1986, 1991; Xu and Stoltz 1991) and a bracovirus (Stoltz et al. unpublished data). It now seems reasonable to assume that the linear, chromosomal, copies of polydnavirus genome segments may serve as templates for the replication of the circular DNAs which ultimately become packaged into virus particles (Stoltz 1990; Fleming and Summers 1991; Xu and Stoltz 1991).

As mentioned previously, polydnavirus particles are designed for delivery into parasitized insects; here, the circular form of polydnavirus DNA establishes what amounts to a genetic colonization of the host animal. Comprising this second arm of the polydnavirus life cycle are the following elements: rapid entry of virions into a variety of host tissues (Stoltz and Vinson 1979a), uncoating of viral nucleic acid either at or within cell nuclei (Stoltz and Vinson 1979a), persistence of viral genome segments throughout the entire course of parasitoid development (Theilmann and Summers 1986; Stoltz et al. 1986), and virus-specific transcription (Fleming et al. 1983; Blissard et al. 1986a, 1986b; Theilmann and Summers 1988; Stoltz et al. 1988b), all in the absence of viral replication. The ultimate purpose of these activities, presumably, is to ensure successful parasitism. This conclusion has been drawn from considerable experimentation, the results of which have conclusively

demonstrated that polydnavirus particles are in most cases absolutely required for successful parasitism (Edson et al. 1981; Stoltz and Guzo 1986; Guzo and Stoltz 1987). There is good evidence, albeit circumstantial, that transcriptional activity is also a requirement (Stoltz and Guzo 1986; Guzo and Stoltz 1987). As yet, no biological activity has been associated with any polydnavirus gene product; however, that is surely only a matter of time. Since polydnaviruses are generally immunosuppressive in host insects (Edson et al. 1981; Stoltz and Guzo 1986; Guzo and Stoltz 1987), it can reasonably be assumed that host defenses represent a primary and perhaps continuing target for virus-specific gene expression. In addition, it may be assumed that polydnaviruses may exert profound effects on other aspects of host physiology, so as to make that more compatible with the needs of developing parasitoid eggs and/or larvae. In keeping with this assumption, we note that a bewildering variety of biological events have now been ascribed to the activity (direct or indirect) of polydnaviruses; these are listed in Table 3, and have been described elsewhere in some detail (Stoltz in press).

Being immunosuppressive, the polydnaviruses may provide particularly useful tools with which to examine the nature of invertebrate immune responses, a subject which has in recent years received increasing attention. Immunosuppression appears to be due, at least in part, to changes in hemocyte number, behaviour, and/or viability (Stoltz and Guzo 1986; Davies et al. 1987; Guzo and Stoltz 1987; Wago and Tanaka 1989), but the molecular basis for these effects remains to be elucidated. In addition, it is not yet clear whether similar mechanisms operate to protect both eggs and larvae. In one study, the restoration of an immune response against yeast cells had no apparent effect on developing parasitoid larvae (Stoltz and Guzo 1986); again, the basis for an apparently selective immunosuppression in such systems is not understood. It is of course quite possible that in some systems the larval surface is not seen as foreign, while the egg is (or vice versa). In any case, it is clear that an investigation of host/parasitoid interactions at the cell/molecular level can be expected to shed new light on some fundamental entomological questions.

Origins.—Where did the polydnaviruses come from? At present, one can only speculate. There are two principal possibilities: 1) they arose from the parasitoid genome itself or, 2) they originally ex-

Table 3. Physiological changes in host animals attributed to the presence of polydnaviruses and virus-like agents (modified from Stoltz (in press)).

Activity	References
Suppression of cellular immune response	Salt 1970 (VLP); Vinson 1977; Edson et al. 1981 (V); Rizki and Rizki 1984 and 1990 (VLP); Guzo and Stoltz 1985, 1987; Stoltz and Guzo 1986 (V); Vinson, Stoltz 1986 (V); Feddersen and Schmidt 1986 (VLP); Tanaka 1987; Strand and Wong 1991 (V).
Inhibition of weight gain	Vinson et al. 1979 (V).
Changes in hemocyte count or behaviour	Rizki and Rizki 1984, 1990 (VLP); Stoltz and Guzo 1986; Guzo and Stoltz 1987; Tanaka 1987; Davies et al. 1987 (V); Wago and Tanaka 1989; Strand and Wong 1991 (V); Stoltz and Beckage (V; unpublished data).
Appearance of new hemolymph polypeptides	Cook et al. 1984 (V); Beckage et al. 1987.
Inhibition of phenoloxidase activity	Stoltz and Cook 1983 (V); Beckage et al. 1990 (V).
Inhibition of protein storage in fat body	Tanaka 1986.
Reduction in hemolymph viscosity	Davies et al. 1987 (V); Stoltz (unpublished data).
Change in hemolymph trehalose concentration	Dahlman and Vinson 1977.
Degeneration of hemopoietic tissue	Guzo and Stoltz 1987.
Pigmentation changes	Beckage et al. 1990 (V).
Degeneration of the prothoracic gland	Dover et al. 1988a (V).
Prolongation and/or arrest of development	Tanaka 1987; Dover et al. 1988b (V); Tanaka and Vinson 1991a; Strand and Dover 1991 (V).
Perturbation of hormone levels	Dover et al. 1987, 1988 (V); Tanaka and Vinson 1991b.

V = gradient-purified polydnavirus used (otherwise, calyx fluid). VLP= virus-like particle. It should be noted that venom is required for full activity of some braconid polydnaviruses (e.g. Kitano 1982; Stoltz et al. 1988b).

isted as typical viruses¹ (Whitfield 1990). While there is no easy way to assess the relative merits of these scenarios, the latter is perhaps more satisfying for a number of reasons. First, there are striking parallels between bracoviruses and the well-known insect baculoviruses. For example, the diameter and overall appearance of the capsid is similar (Stoltz and Vinson 1979a); in both cases, the envelope may surround nucleocapsids either individually or in groups; in addition, some bracovirus nucleocapsids are fully as long as baculovirus nucleocapsids (Stoltz et al. 1976); finally, uncoating of both bracovirus and granulosis virus nucleocapsids occurs at nuclear pores (Summers 1969; Stoltz and Vinson 1979b). While these may represent examples of convergent evolution, it is just as reasonable to suppose that some sort of stable relationship arose between a progenitor baculovirus and the parasitoid reproductive tract, and that some such relationship ultimately gave rise to the bracoviruses. In this regard, it is of interest to note

that such a relationship apparently exists between a baculovirus and the ichneumonid parasitoid, *Mesoleius tenthredinis* (Stoltz 1981); as with the bracoviruses, all females thus far examined appear to carry virus, and replication is apparently restricted to the parasitoid ovary. Further characterization of this interesting system should be given high priority. Finally, defective interfering (DI) forms of baculoviruses have recently been discovered (Kool et al. 1991; Krell, pers. commun.). DI particles contain sub-genomic nucleic acid molecules, and have been known to ameliorate the severity of viral disease (Dimmock and Barrett 1986). Conceivably, non-pathogenic bracovirus

¹For the purpose of this discussion, typical viruses are those for which there exist hosts susceptible to productive infection (thus generating progeny virus particles). In the case of the polydnaviruses, however, all hosts permissive for viral replication already carry the viral genome, that being transmitted as a provirus.

genomes could have evolved from defective interfering baculovirus particles.

The bracoviruses and ichnoviruses have been assigned to the same virus family because of similarities in both genome organization and life cycle. It should be stressed, however, that this does not mean that the family is necessarily monophyletic. If monophyletic, then the polydnaviruses must have arisen from a common ancestor, which could have been either a virus or an appropriate collection of parasitoid genes. This hypothesis does not, however, readily account for the major structural differences which define the two polydnavirus subgroups (see Fig. 1). Alternatively, the braco- and ichnoviruses could have arisen from entirely different types of viruses, with extant similarities resulting from convergent evolution. It could be argued that, for the latter to have occurred, the ovary should be a favoured site for *non-cytopathic* virus replication; in fact, as we have seen (Table 1), this would certainly appear to be the case. The establishment of a variety of non-pathogenic viral agents in the parasitoid ovary could then be seen as a prerequisite for the origin of ancestral polydnavirus/parasitoid complexes. Variations on this theme might also have given rise to the *Venturia* and *Leptopilina* particles, among others waiting to be described.

The polydnavirus/parasitoid relationship is undoubtedly ancient, at least in terms of origin(s). Thus it is reasonable to assume that during its establishment, opportunities must have existed for genetic transfer between viral and host genomes as (we suppose) they co-evolved to become a single genome. Indeed, it could generally be argued that the establishment of a genetic fusion between two originally separate entities (e.g., mitochondria and eukaryotes) might require that some functions be transferred from one to the other, and vice versa. One might predict, for example, that some genes required for viral morphogenesis might have lost encapsidation signals: since morphogenesis occurs only in the wasp ovary, there would be no point in packaging such genes for expression in the parasitized host. Similarly, parasitoid genes promoting successful parasitism might more usefully have become incorporated into the viral genome, to be subsequently delivered to parasitized insects. It is of considerable interest in this regard to note that the ichnovirus, CsV, is thought to have acquired a parasitoid venom gland gene, which is duly expressed in parasitized host larvae (Webb and

Summers 1990).

Implications for Parasitoid Systematics.— Given that polydnavirus DNA is apparently transmitted in a stable Mendelian fashion, it cannot logically be regarded as differing in any significant way from parasitoid genomic DNA. Put more directly, when we examine polydnavirus DNA, we are also examining parasitoid DNA. It follows that relationships among the polydnaviruses should parallel those among the parasitoids with which they are associated. It may thus be instructive to consider what little is known at present about polydnavirus relationships in the context of parasitoid systematics.

It is of interest in this regard to note an apparent congruence of classical taxonomic determinations with the results of previous electron microscopic studies. Early work clearly established the existence of two bracovirus morphotypes, distinguished on the basis of whether one or several nucleocapsids were enclosed within the viral envelope (see Figure 1). Within members of the (former) genus *Apanteles*, these two morphotypes were represented in roughly equivalent numbers, suggesting—in hindsight—that the genus could well be polyphyletic, or that at least one biologically relevant division might be found within the genus. In Table 4, information on bracovirus morphology is presented in relation to Mason's (1981) reclassification of *Apanteles*. Interestingly, those genera which Mason assigned to the tribe Cotesiini are for the most part characterized by polydnaviruses in which nucleocapsids are not individually enveloped; of 5 such genera for which data are presently available, only one (*Diolcogaster*) seems out of place: unlike all other Cotesiini thus far examined, polydnavirus nucleocapsids in *Diolcogaster* are individually enveloped. It might, accordingly, be suggested that the taxonomic position of *Diolcogaster* could profitably be reconsidered. Alternatively, absence of an individual envelope for each viral nucleocapsid might represent a synapomorphy for a lineage somewhat less inclusive than the Cotesiini as a whole.

Additional information may in future be derived from analyses of viral DNA. For phylogenetic inference, such studies should ideally incorporate an analysis of sequence data from both wasps and viruses (see below). Thus far, our studies have been limited to the identification of shared (or greatly similar) genome segments between wasp taxa, using nucleic acid hybridization/blotting techniques. This approach can provide some indi-

cation of which taxa share genetically similar polydnaviruses, although the data obtained are not directly useful for phylogenetic studies because no distinction can be made between ancestral and derived similarities. Some observations are already available (Figures 4 and 5); these are provided here merely as preliminary indication of a possible correspondence between wasp and virus relationships. In Figure 4, polydnavirus DNA circles (i.e., genome segments) from a variety of braconid parasitoids have been electrophoretically separated and then probed with ^{32}P -labelled DNA from *Cotesia melanoscela*. Hybridization signals were detected only within members of the same genus; no hybridization signal was detected even in the case of *Glyptapanteles*, which, according to Mason (1981), belongs to the same tribe as *Cotesia*. Our results, as far as they go, are therefore entirely in accord with Mason's generic division of *Apanteles*. Parenthetically, it should be noted that while both *C. melanoscela* and *G. flavicoxis* (Marsh) are gypsy moth parasitoids, their respective polydnaviruses are quite dissimilar; thus there is no indication that host-sharing influences the identity of the viruses

carried by these two parasitoid species. It is therefore reasonable to assume that their cognate polydnaviruses likely engage the same host milieu in rather different ways. Conversely, where two viruses show significant sequence homology, we might reasonably predict that shared gene products are interacting with common host targets. In any case, it will be of considerable interest to extend the DNA studies so as to include additional genera; in combination with analyses of wasp morphological and molecular data, this may permit a further refinement of microgastrine classification. The development of new data in a timely fashion could prove particularly useful for this group, since Mason's (1981) work on this group is currently undergoing reappraisal (Walker et al. 1990; Mason and Whitfield in preparation).

Preliminary studies involving ichneumonid polydnaviruses (ichnoviruses) are equally interesting, while nevertheless somewhat more difficult to interpret because of uncertainties in the current generic classification (see, e.g., discussion by Wahl 1987). Even so, some inferences may reasonably be drawn from already available, if limited, data: for



Fig. 4. DNA homologies among polydnaviruses from different braconid genera. A and B represent gel and Southern blot, respectively, of viral DNAs extracted from calyx fluids from the following: *Cotesia melanoscela*, *C. marginiventris*, *Microplitis croceipes*, and *Cardiophiles nigricipes* (lanes 1 to 4, respectively). The blot was probed overnight under conditions of high stringency (68°C , $0.5\text{ M Na-phosphate}$, $\text{pH } 7.2$, containing 7% SDS) using $2.5 \times 10^5\text{ cpm/ml}$ of ^{32}P -labelled whole viral DNA from *C. melanoscela*. Exposure was for 24 hrs

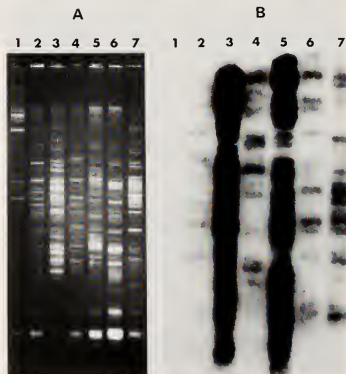


Fig. 5. DNA homologies among polydnaviruses from 5 different ichneumonid genera. A and B represent gel and Southern blot, respectively, of viral DNAs extracted from calyx fluids of the following: *Campeletis* sp., *Diadegma* sp., *Hyposoter fugitivus*, *H. annulipes*, *H. lynmantriae*, *Diadegma terebrans*, and *Olesicampe geniculatae* (lanes 1 to 7, respectively). Experimental conditions were as given in Fig. 4, except that the probe used here was ^{32}P -labelled *H. fugitivus* whole viral DNA.

Table 4. An apparent congruence of taxonomic assignments made on the basis of viral and parasitoid morphology in the Microgasterinae. In most cases, only a single species has been examined by electron microscopy. Exceptions are *Apanteles*, *Glyptapanteles* and *Cotesia*, in which respectively two, three and nine species have been examined (see Table 2).

VIRUS	PARASITOID	
	genus ²	tribe
# nucleocapsids/ envelope ¹		
1	<i>Apanteles</i>	Apantelini
1	<i>Pholetesor</i>	Apantelini
1	<i>Microgaster</i>	Microgasterini
1	<i>Hypomicrogaster</i>	Microgasterini
1	<i>Clarkinella</i>	Microgasterini
1	<i>Microplitis</i>	Microplitini
several	<i>Cotesia</i>	Cotesiini
several	<i>Glyptapanteles</i>	Cotesiini
several	<i>Protapanteles</i>	Cotesiini
several	<i>Protomicroplitis</i>	Cotesiini
1	<i>Diolcogaster</i>	Cotesiini

¹ Stoltz and Vinson (1977) and unpublished data.

² Genera and tribes here listed are as given by Mason (1981), whose revision of *Apanteles* was based primarily on parasitoid morphology. It should be noted that all of the genera now listed under Cotesiini were formerly included within the single genus *Apanteles*. An additional analysis of the tribes has been published by Walker et al. (1990).

example, probing viral DNA from various wasp taxa with a particular viral genome segment can suggest, at least in certain cases, that some species (within a particular genus) might be more closely related than others. Our admittedly limited studies (Figure 5) would seem to suggest that polydnvirus DNAs from *Hyposoter fugitivus* and *H. lymantriae* are much more similar to each other than to those from some other species assigned to the same genus. Note also that representative viruses from three different campoplegine genera (*Hyposoter*, *Diadegma* and *Olesicampe*) would seem to be related. Viruses from certain other genera (e.g., *Campoletis*) appear to be only distantly related, if at all, to the "Hyposoter group" identified here (i.e., *Hyposoter*, *Diadegma*, *Olesicampe*). Much the same kind of information was developed in an earlier study in which viral antigens were compared by immunoblotting (Cook and Stoltz 1983). Additional work along these lines may ultimately prove useful in helping to refine the difficult taxonomy of ichneumonid (especially campoplegine) parasitoids.

Obviously, more useful molecular data for phylogenetic analysis will be derived from the

actual sequencing of viral DNA, which would provide a more direct assessment of homologies or differences in DNA sequence (Hillis et al. 1990; Swofford and Olsen 1990), and would allow polarization of characters via outgroup analysis. Presently, with the single exception of *Campoletis sonorensis* virus (CsV), so little is known about polydnvirus DNA sequences that primers for the polymerase chain reaction (which allow for easy isolation of homologous regions of DNA - see, e.g. White et al. 1989) are not generally available. A substantial number of *H. fugitivus* polydnvirus genome segments have now been cloned (Xu and Stoltz 1991) and many of these have been used as probes vs. other parasitoid taxa (Xu and Stoltz, unpublished data); some cross-hybridize significantly and may therefore contain conserved sequences. We would predict that genes potentially encoding conserved domains will include those required for the replication and encapsidation of polydnvirus genomes. Identification and characterization of such genes will be necessary for an elucidation of viral interrelationships; it is our hope that knowledge concerning the latter will ultimately prove useful in establishing a linkage, assuming one exists, between viral and parasitoid phylogenies.

CONCLUDING REMARKS

We have argued above that the study of polydnviruses may be relevant, perhaps significantly, to the systematics of at least some groups of the parasitic Hymenoptera. There are additional benefits to be gained from studying these and other parasitoid-associated viruses; these derive from the ways in which they are identified and examined: typically, electron microscopy and agarose gel electrophoresis (of encapsidated viral DNA). Both of these procedures require that the reproductive tract be dissected out from adult female parasitoids, thus affording an opportunity to examine the morphology of the ovary and its accessory glands. This kind of information has already proven extremely useful to systematists (Pampel 1913; D'Rozario 1942; Iwata 1959, 1960; Robertson 1968; Edson and Vinson 1979; Edson et al. 1982; Maeto 1987). Electron microscopy, in particular, may add a new dimension to what is already known.

If it could ever be shown that genetic relationships among the polydnviruses run parallel to the phylogeny of their parasitoid carriers, if only in part, then perhaps knowledge of one might have

predictive significance for the other. For example, polydnaviruses in *Hyposoter* and *Olesicampe* would appear to be relatively closely related (Cook and Stoltz, 1983, and present report). Yet, the parasitoids which carry them attack quite dissimilar hosts: Lepidoptera and Hymenoptera, respectively. Should we assume that these viruses are nonetheless doing something very similar in these disparate hosts, and if so, what? Answers to such questions could well prove intriguing. This situation may be contrasted with that previously discussed, in which two apparently unrelated viruses (from *C. melanoscela* and *G. flavicoxis*) nevertheless find themselves interacting (how?) with identical host larvae (*L. dispar*).

At this point, it may perhaps suffice to suggest that much more work needs to be carried out on the taxonomic and biological diversity of polydnaviruses (and other viruses and virus-like agents) associated with hymenopteran parasitoids. Coincident with this need is a pressing demand for more work on the systematics of the parasitic Hymenoptera. We predict that these two agendas could be mutually informative.

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**A New Southern African Species of the Genus *Celonites* Latreille
(Hymenoptera: Vespidae, Masarinae)
Associated with the Flowers of *Wahlenbergia* (Campanulaceae)**

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Abstract.—A new southern African species of the genus *Celonites* Latreille (Hymenoptera, Vespidae, Masarinae) associated with the flowers of *Wahlenbergia* Schrad. ex Roth (Campanulaceae) is described. Comparisons are drawn between the new species, *C. latitarsis*, and previously known *Celonites* species. The form of the fore tarsomeres of *C. latitarsis* is distinctive.

The writing of the present paper is occasioned by the need to provide a name for a hitherto undescribed species of *Celonites* Latreille the nesting of which is described in a forthcoming paper by Gess and Gess. The new species, described from the Clanwilliam District of the western Cape Province of South Africa, occurs sympatrically with two other species, *C. wahlenbergiae* Gess and *C. bergenvahliae* Gess, previously described from that area (Gess 1989) and like those species shows a predilection for the flowers of species of *Wahlenbergia* Schrad. ex Roth (Campanulaceae).

***Celonites latitarsis* Gess, new species**

Female.—(Figs 1, 2 and 3). Black; distal half of mandibles, entire pronotum, tegulae, declivous parts of scutellum to variable extent, occasionally metanotum medially, terga 1-3 (except anterior declivous face of tergum 1 and normally covered basal transverse bands on terga 2 and 3), sterna 1-3, extreme distal ends of femora, tibiae and tarsi of all legs (except for a dark longitudinal streak on fore-tibiae), reddish-brown. No yellowish-white markings anywhere.

Wings moderately browned. Length 8.5 mm; length of extended tongue 4.2 mm; length of fore wing 5.6 mm; hamuli 10.

Head (Fig. 1); frons coarsely, closely and in places subconfluently punctured and on each side somewhat downwardly substrigate towards an impressed median line below anterior ocellus, with an indication of a raised but not carinate transverse ridge or swelling which is strongest above antennal insertions but almost obliterated medially and

does not extend into ocular sinuses laterally. Clypeus finely and sparsely punctured and transversely strigulate in a more or less downwardly curved arc; clypeal disc fairly strongly raised above level of eyes and evenly convex over most of its surface other than laterally where slightly depressed or concave, without any indication of a carina.

Pronotum, mesonotum, scutellum, and dorso-lateral areas of propodeum coarsely and densely punctured; the sides of the pronotum and the mesopleura longitudinally ridged, the mesopleura strongly so. Scutellum medially convex, strongly raised above level of mesonotum, with a wide crenulate anterior furrow and a marked median longitudinal groove.

Propodeal lamella (Fig. 2) of each side wide, broadly truncate distally, with outer edge gently convex, separated from the median part of the propodeum by an inwardly curving slit ending in a relatively large subcircular emargination; lateral projection of the ventral margin on each side of the median part of the propodeum with its hind edge slightly bent forward and with its point narrowly rounded, about as wide as long, and projecting across opening of curved slit a little anterior to level of end of lamella (i.e. intermediate in form between that of *C. wahlenbergiae* and *C. bergenvahliae*).

Gastral terga coarsely and densely punctured, with their posterior margins smooth; terga 1-5 with posterior outer angles moderately projecting; tergum 6 medially somewhat pointedly produced and apically narrowly rounded, moderately emarginate before sides and with lateral margins angular.

Gastral sterna shiny; sterna 2-5 with moderate

punctures scattered over disc but closer on postero-lateral corners, with finer punctures scattered on interstices and with intermediately-sized punctures forming very narrow subapical transverse bands; sternum 6 with moderate close punctures.

Fore tarsi (Fig.3) with all but first tarsomere expanded; tarsomeres 2-4 and more particularly 3 and 4 markedly asymmetrical, their posterior (outer) distal corners produced; tarsomere 5 depressed, seven-tenths as wide in the middle as long and with its sides strongly and symmetrically biconvex.

Male.—(Figs 4 and 5). Black; distal half of mandibles, flagellomeres 2-5 (in one specimen only), hind margin and dorsal aspect of pronotum to variable extent (in one specimen hind margin narrowly and medially only), most of tegulae, extreme postero-lateral margins of scutellum, terga 1-3 to variable extent (ranging from broad transverse distal bands reaching sides on terga 1 and 2 but not reaching sides on tergum 3, to narrow transverse distal band not quite reaching sides on tergum 1 and a short transverse distal mark medially on tergum 2), extreme distal ends of femora, tibiae and tarsi of all legs (except for a dark longitudinal streak on fore-tibiae or on all tibiae), reddish brown. No yellowish-white markings anywhere, not even on face, clypeus or labrum.

Wings moderately bawned. Length 7.1 mm; length of extended tongue 3.4 mm; length of fore wing 4.5 mm; hamuli 7.

Structure much like that of female differing most noticeably with respect to the following: antennal club wider with individual flagellomeres less discernible and with three sensory depressions set in a groove beneath; eyes closer below; clypeus narrower and more strongly convex; frons with raised transverse ridge or swelling stronger especially medially; terga with posterior outer angles more strongly projecting; tergum 7 compared to tergum 6 of female with median part more widely rounded and with lateral emarginations much better developed (due to strong development of posterior outer angles).

Genitalia (Fig 5); parameres wide, not emarginate, distally somewhat outwardly produced and apically rounded, furnished beneath with a profusion of long and strong inwardly directed curved hairs.

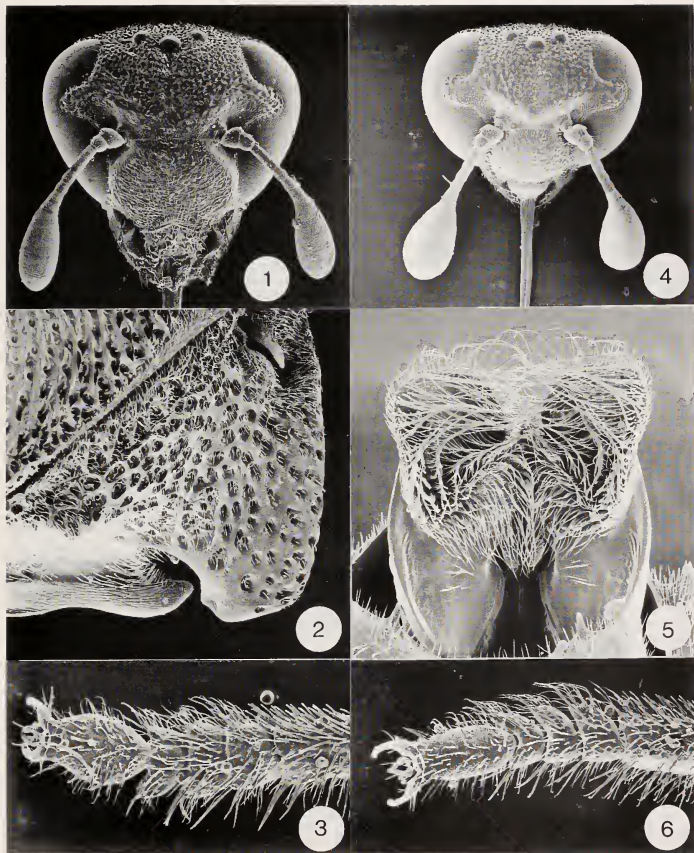
Material examined.—Cape Province: Clanwilliam District, 11 km W of Clanwilliam on road to Graafwater, 17.x.1989, 1 female paratype and 1

male paratype (in flowers of *Wahlenbergia psammophila* Schltr., Campanulaceae), 1 female paratype (on ground); same locality, 2-8.x.1990, 1 female paratype (nesting), Holotype female and 1 male paratype (in flowers of *Wahlenbergia psammophila*, Campanulaceae), 1 female Paratype and 1 male paratype (on ground) and 1 male paratype (on flowers of *Coclanthum grandiflorum* E. Mey. ex Fenzl, Aizoaceae) (all F.W. and S.K.Gess). The type material is deposited in the Albany Museum.

Discussion.—*Celonites latitarsis* is superficially similar to both *C. wahlenbergiae* Gess and *C. bergenwaliae* Gess in the company of which it was found at the locality given above. In the field the total absence of any yellowish-white markings on the pronotum and terga readily distinguishes the female from that of *C. wahlenbergiae* and from at least some females of *C. bergenwaliae*; the black face, clypeus and labrum of the male immediately distinguishes it from the males of both other species.

Less immediately obvious but important differences are the following: in both sexes the sculpturing of the head is coarser (compare Figs 1 and 4 with Gess 1989: Figs 6-9). In the female the form of the fore tarsomeres (Fig.3) sets *C. latitarsis* apart not only from *C. wahlenbergiae* and *C. bergenwaliae* but also from ten other southern African *Celonites* species (including 4 as yet undescribed species). Overall the tarsi are more robust and are markedly expanded. In detail they differ in that their asymmetry results from tarsomeres 2-4 being produced distally at their posterior (outer) corners rather than at their anterior (inner) corners (compare Figs 3 and 6). In this the tarsi of *C. latitarsis* differ also from those of female Masarinae in general. Associated with the distal posterior (outer) corners of tarsomeres 1-4 are a number of strong stiff bristles which contrast with the other hairs on the tarsomeres. Such bristles are less strongly and less obviously developed in *C. wahlenbergiae* and are totally lacking from the tarsomeres of species such as *C. andrei*, *C. capensis*, *C. clypeatus* and *C. promontorii* which are covered with uniform dense woolly hairs. The unique form of the tarsomeres of *C. latitarsis* is associated with unusual nesting behaviour including sand raking during nest construction (Gess and Gess 1992).

In the male the groove on the underside of the antennal club extends over almost its full length, distally exceeding the third sensory depression by more than the length of the latter, and is clearly



Figs. 1-6. *Celonites latitarsis*. 1, Frontal view of head of female (x 20). 2, Dorsal view of right half of propodeum of female showing lamella (x 65). 3, Left fore tarsus of female (x 75). 4, Frontal view of head of male (x 20). 5, Ventral view of genitalia of male (x 80). 6, *C. wahlenbergiae*, left fore tarsus of female (x 75).

visible when the club is viewed end-on. In *C. wahlenbergiae* and *C. bergenwaliae* the groove is wider and shallower, does not much extend beyond the third sensory depression and is only very weakly indicated when the club is viewed end-on. The male genitalia differ in that the parameres are rounded distally (Fig 5) whereas in the other two species they are emarginate (see Gess 1989: Figs 11 and 13).

Etymology.—The name *latitarsis* serves to draw attention to the wide fore tarsomeres of the female.

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**Ethology of Three Southern African Ground Nesting Masarinae,
Two *Celonites* Species and a Silk-spinning *Quartinia* Species,
with a Discussion of Nesting by the Subfamily as a Whole
(Hymenoptera: Vespidae)**

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Abstract.—Accounts are given of some aspects of the nesting of *Celonites latitarsis* Gess, *C. wahlenbergiae* Gess and *Quartinia vagepunctata* Schulthess. *Celonites latitarsis* nests in sandy soil, excavating a sloping burrow terminating in a cell in which it constructs an earthen cell. *C. wahlenbergiae* uses a pre-existing burrow in which it constructs linearly arranged earthen cells. Both species collect soil for cell construction from a quarry at some distance from the nest and circumstantial evidence suggests that both use nectar as the bonding agent. *Quartinia vagepunctata* excavates a vertical burrow surmounted by a turret and terminating in a cell, the whole being stabilized by the use of self generated silk as the bonding agent. In order that the nesting accounts should be put into context, nesting by the Masarinae (*sensu* Carpenter 1982) as a whole is outlined and discussed.

Celonites Latreille and *Quartinia* Ed. André are two Old World masarine genera. *Celonites* occurs in the Palaearctic Region in the countries bordering the Mediterranean Sea, northwards to Switzerland and southern Germany and eastwards to Transcaspia and south-western Iran, and in the Afrotropical Region in north-east Africa and southern Africa (Richards 1962). In southern Africa the genus has a southern and western distribution with the greatest number of species having been recorded from the western areas (Richards 1962, Gess and Gess 1989, label data Albany Museum).

Around thirty species of *Celonites* are known, nearly half from southern Africa. Little has been recorded concerning their nesting behaviour due undoubtedly to the cryptic nature of the nests. Brief notes have been published on the nests, all aerial, of six species as listed in the discussion. It seemed likely that *Celonites* as a genus would be found to construct aerial nests. The present accounts of ground nesting by *C. latitarsis* Gess and *C. wahlenbergiae* Gess therefore, although based on only one nest each, add considerably to the knowledge of the nesting behaviour of the genus.

Quartinia occurs in the Palaearctic Region bordering the Mediterranean Sea and extends east-

wards into Asiatic Russia and India, and in the Afrotropical Region in southern Africa (Richards 1962). In southern Africa the genus has a largely southern and western distribution with, like *Celonites* the greatest number of species having been recorded from the western areas (Richards 1962, Gess and Gess 1989, label data Albany Museum).

Around fifty species of *Quartinia* are known, more than half from southern Africa. Concerning the nesting behaviour of this genus there seems to be only one casual observation listed in the discussion. The present account for *Q. vagepunctata* Schulthess, which uses silk for stabilizing its turret, burrow and cell walls is therefore of particular interest.

The investigations presented in the present paper were undertaken during the course of two field trips to the southwestern Cape in early summer, September/October, of 1989 and 1990.

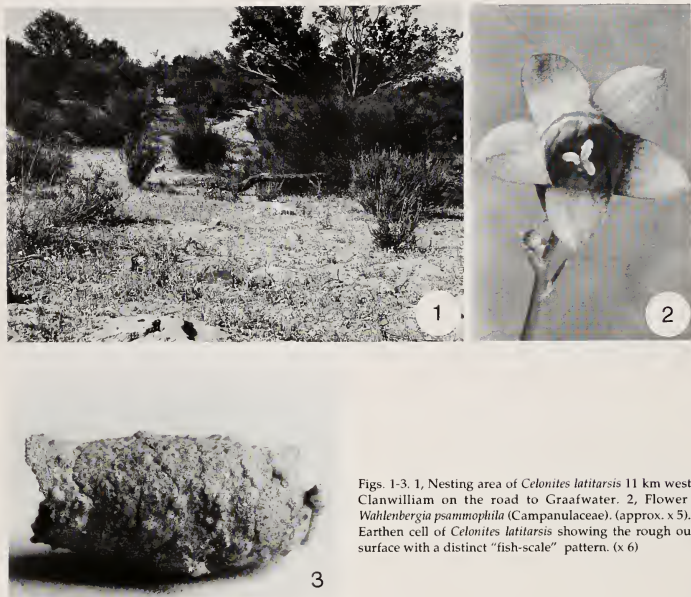
Voucher specimens from these studies are deposited in the Albany Museum.

ETHOLOGICAL ACCOUNTS

***Celonites latitarsis* Gess**

Geographic distribution and description of nesting area.—*Celonites latitarsis* has as yet only been recorded from the type locality, 11 km west of Clanwilliam on the road to Graafwater (Fig. 1) in

¹The order of names is alphabetical and equal joint authorship should be understood.



Figs. 1-3. 1, Nesting area of *Celonites latitarsis* 11 km west of Clanwilliam on the road to Graafwater. 2, Flower of *Wahlenbergia psammophila* (Campanulaceae). (approx. x 5). 3, Earthen cell of *Celonites latitarsis* showing the rough outer surface with a distinct "fish-scale" pattern. (x 6)

the hilly area between the Olifant's River Valley and the sandy coastal plain.

The vegetation is characterized by the presence of Restionaceae, shrubby Proteaceae and scattered *Aspalathus spinescens* Thunb. (Fabaceae) with a sparse general ground cover of predominantly *Wahlenbergia psammophila* Schltr. (Campanulaceae) and *Helichrysum* cf. *hebelepis* DC. (Asteraceae), and a moist ground cover of *Monopsis debilis* (L.f.) Presl. (Lobeliaceae). It is best categorized as "Dry Mountain Fynbos", as described by Moll et al. (1984), with an intrusion of sandveld elements on disturbed ground.

The soil is sandy, relatively coarse and loose on the surface but finer and more compact beneath. The finer sand is brought to the surface by the Cape Dune Molerat, *Bathergus suillus* (Schreber) (Bathyergidae) which is common in the area. The molehills stabilize forming "hillocks" of compacted

sand suitable for the excavation of burrows and used for this purpose by *Scapter* (Colletidae), *Belomicrus* and *Bembecinus* (both Sphecidae). The nest of *C. latitarsis* was sited in the gently sloping side of such a "hillock" which was almost entirely covered with loose sand and was sited at the base of a small, dry, dead shrub.

Plant visiting.— All plants in flower were sampled for flower visitors. Females and males of *C. latitarsis* were visiting flowers of *Wahlenbergia psammophila* (Fig. 2) in company with *Celonites wahlenbergiae* Gess, *Celonites bergenwaliae* Gess and *Masarina mixta* Richards (also Masarinae). Apart from *W. psammophila* the only plant species from which *C. latitarsis* was recorded was *Coelanthum grandiflorum* E. Mey ex Fenzl (Aizoaceae) (1 male).

On sunny days activity on *W. psammophila* flowers was from mid morning, when the flowers opened, until late afternoon, when the flowers

closed. The exact times of flower opening and closing and masarine activity varied according to the weather.

Females of *C. latitarsis* visiting *W. psammophila* flowers entered up to eight flowers in succession, usually on different plants. They always alighted on the outwardly curved free tip of a corolla lobe before entering the flower.

Provision.— Pollen from the provision taken from the nest and examined microscopically was all of one type and matched that of *W. psammophila*.

Description of nest.— Only one nest of *C. latitarsis* was located. It consisted of an arched entrance leading to a short sloping burrow of diameter 4.5 mm terminating at a depth of 35 mm in a horizontal excavated cell of diameter 5 mm. Within the excavated cell was a constructed earthen cell of the same diameter as the excavated cell (Figs 3 and 4).

The earthen cell is roughly ovoid with a slightly flared lip extending beyond the neck. It is 10–11 mm in length, the lip being uneven. The outer diameter at the widest point is 5 mm and at the neck 4 mm. The cell walls are extremely hard, the sand grains being very firmly cemented together. The outer surface is rough and has a visible "fish scale" pattern. The inner surface is smoothed. The cell is still open, provisioning not having been completed.

Method of construction of the nest, oviposition and provisioning.— There are two distinct phases in nest construction; burrow excavation and cell construction. Sand removed during burrow excavation is not used for cell construction. Sand for this purpose is mined at some distance and carried into the burrow. The burrow entrance is left open while the wasp is away from the nest.

At 11h00 on 3.x.1990 a female *C. latitarsis* was seen to be initiating a burrow. Sand excavated from the burrow was drawn out by the wasp as she reversed out of the burrow to a distance of approximately 20 mm down slope from the burrow entrance, where it accumulated forming a tumulus. From time to time a certain amount of raking of the "path" to the burrow took place. Also from time to time the wasp flew up, circled and returned.

At 11h52 burrow excavation had been completed and cell construction commenced. During cell construction the wasp made regular visits to a quarry site on a stabilized molarat "hillock" approximately 2.5 m from the nest. When at the quarry site, the wasp vibrated up and down vigorously whilst scraping up a load of sand. The visits to the quarry, each taking an average of 29

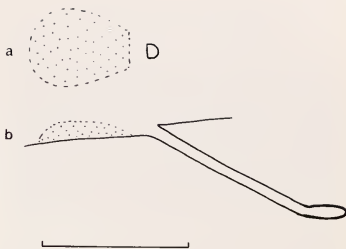


Fig. 4. Diagrams of nest of *Celonites latitarsis*: a. nest entrance and tumulus from above; b. vertical plan. (Scale bar = 50 mm).

seconds ($n = 36$), alternated regularly with periods in the nest. Each period in the nest during which the building material must have been added to the cell lasted an average of 48 seconds ($n = 37$). After five to seven successive visits to the quarry the wasp visited a succession of *W. psammophila* flowers and was then lost to sight for 10–20 minutes. On her return she alighted at either the nest or the quarry site. It is presumed that she was collecting liquid to mix with the dry sand to make it malleable for cell construction. As the cell walls are harder and more durable than they would be had water been used and as *C. latitarsis* has never been observed at water it seems probable that the liquid collected was *W. psammophila* nectar.

At 14h00 after approximately 36 additions to the cell, the wasp flew off to visit a succession of *W. psammophila* flowers. After an absence of 49 minutes she reappeared. Instead of going to the quarry she returned directly to the nest. After a period of 11 minutes 45 seconds in the nest, during which it is probable that oviposition took place, she flew off to the flowers. Provisioning had commenced. A regular pattern of flower visiting alternating with a period in the nest continued until 16h00 when the wasp entered the nest and did not reappear.

At 17h00 it was decided that the wasp's work for the day was over. The nest was then investigated and the female which was sheltering in the cell was collected.

Male behaviour.— No males were seen in the vicinity of the nest.

Celonites wahlenbergiae Gess

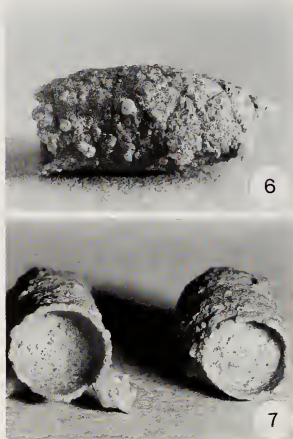
Geographic distribution and description of nesting area.— *Celonites wahlenbergiae* Gess has been recorded from three sites in the Clanwilliam District, one at the Clanwilliam Dam and two on the road to Graafwater at 5 km and 11 km west of Clanwilliam. At all sites it has been associated with *Wahlenbergia*. Despite intensive collecting on *Wahlenbergia* in areas beyond the Clanwilliam District it has not been found, suggesting a relatively restricted distribution.

A nesting area of *Celonites wahlenbergiae* was located on the eastern side of the Clanwilliam Dam on a sparsely vegetated slope above the caravan park. The vegetation in the immediate vicinity of Clanwilliam is classified as a "Mosaic of Dry Mountain Fynbos and Karroid Shrublands" (Moll et al. 1984). That of the nesting area of *C. wahlenbergiae* is best described as depauperate dry fynbos. The dominant shrub is *Aspalathus spinescens* Thunb. (Fabaceae). Ground cover is sparse. The dominant low growing plant is *Wahlenbergia paniculata* (Thunb.) A.DC. (Campanulaceae). The soil is of the same nature as that at the *C. latitarsis* nesting site and is similarly subject to mole rat activity.

Plant visiting.— *Celonites wahlenbergiae* has been found commonly associated with deep flowered *Wahlenbergia* species: with *W. paniculata* (as *W. sp.* A in Gess 1989, Gess and Gess 1989) at Clanwilliam Dam; with *Wahlenbergia costata* A.DC. 5 km west of Clanwilliam; and with *Wahlenbergia psammophila* 11 km west of Clanwilliam. In all cases where the wasp was found *Wahlenbergia* was in flower in



Fig. 5. Vertical plan of nest of *Celonites wahlenbergiae*. (Scale bar = 50 mm).



Figs. 6, 7. 6, Earthen cell of *Celonites wahlenbergiae* showing the rough outer surface with a distinct "fish-scale" pattern. (x 6). 7, End on views of the earthen cells of *Celonites wahlenbergiae*. On the left is shown the smoothed inner surface of an incomplete cell; on the right is shown the seal of a completed cell. (x 6).

abundance. It is of interest that the large, shallow flowered, *Wahlenbergia annularis* A.DC., which was flowering abundantly in the areas where *C. wahlenbergiae* was present, was never visited by these wasps although it was visited for nectar and pollen by melittid bees.

Celonites wahlenbergiae, however, is not restricted to *Wahlenbergia* species as it was visiting, in addition but less commonly, *Crassula dichotoma* L. (Crassulaceae) at Clanwilliam Dam; and *Coelanthum grandiflorum* E. Mey ex Fenzl (Aizoaceae), *Herrea* sp. (Mesembryanthemaceae), *Polycarena* sp. (Scrophulariaceae), *Helichrysum* cf. *hebelepis* DC. (Asteraceae), an unidentified composite and *Pelargonium* sp. (Geraniaceae) 11 km west of Clanwilliam. It, however, was not represented in samples of insects from other plants in flower, notably *Aspalathus spinescens* which is commonly visited by the masarines *Ceramius clypeatus* Richards and *Masarina familiaris* Richards.

Provision.— Provision from a fully provisioned cell was olive green, very moist and did not adhere

to nor wet the cell walls. The pollen, examined microscopically, was found to be of two types, one matching only that from *Wahlenbergia paniculata* and the other only that from a *Coelanthum* species which was growing mixed with it.

Description of the nest.— The single nest of *C. wahlenbergiae* located consisted of three linearly arranged earthen cells attached to the wall of an apparently pre-existing burrow excavated in sandy soil. The burrow, of diameter 5.5 mm, descended vertically to a depth of approximately 30 mm after which it continued in a steep slope. Three cells, two sealed and the third in an early stage of construction, were positioned at the upper end of the slope (Fig. 5).

The completed cells are rounded at the inner end, roughly ovoid but with the sealed outer end truncate. They are 9 and 8 mm in length, and 4.5 and 4 mm respectively in outer diameter at the widest point. The outer diameter at the neck of each cell is 4 mm. The cell walls are extremely hard, the sand grains being very firmly cemented together. The outer surface of the cell wall is rough and shows a distinct "fish-scale" pattern (Fig. 6). The seal, constructed from the same material as the cell walls, is positioned within the neck of the cell (Fig. 7). The base of a succeeding cell is attached to the seal of a preceding cell so that it is positioned within the opening of that cell. The inner surface of the cells is smooth (Fig. 7).

Method of construction of the nest.— Nest initiation was not observed. A pre-existing burrow was probably used as the cells in the nest investigated were positioned on the burrow wall well above the inner end of the burrow and as their diameters were less than was that of the shaft.

Sand for construction of the cells was being quarried from the surface of a stabilized molehatch "hillock" situated 3 m from the burrow. At midday on 19.x.1989 the wasp was seen visiting a *Crassula dichotoma* flower after which she flew to the quarry. At the quarry site she vibrated vigorously apparently loosening sand with her mandibles. Having gathered a load she flew with it to the burrow. Sand gathering was repeated several times. The wasp was then captured and the nest investigated.

As the cell walls are harder and more durable than would be expected had water been the bonding agent it is probable that nectar was used. *Celonites wahlenbergiae* has, notably, never been seen at water. It seems likely that the visit to *Crassula dichotoma* was for the purpose of collecting nectar.

Male behaviour.— No males were seen in the vicinity of the nest.

Quartinia vagepunctata Schulthess

Geographic distribution and description of nesting area.— *Quartinia vagepunctata* Schulthess has been recorded from 38 km west of Ceres, Calvinia, and Doorn River Falls (Richards 1962). It is here recorded from two sites on the western fringe of the Great Karoo (above the Nieuwoudtville Waterfall [= Richards' Doorn River Falls] and the Skuinshoogte Pass, 15 km north of Nieuwoudtville) and from six sites in Namaqualand (Goegab Nature Reserve to the east of Springbok; Narap, Klipfontein and the Wildeperdehoek Pass, all to the south west of Springbok; and Anenous to the north west of Springbok).

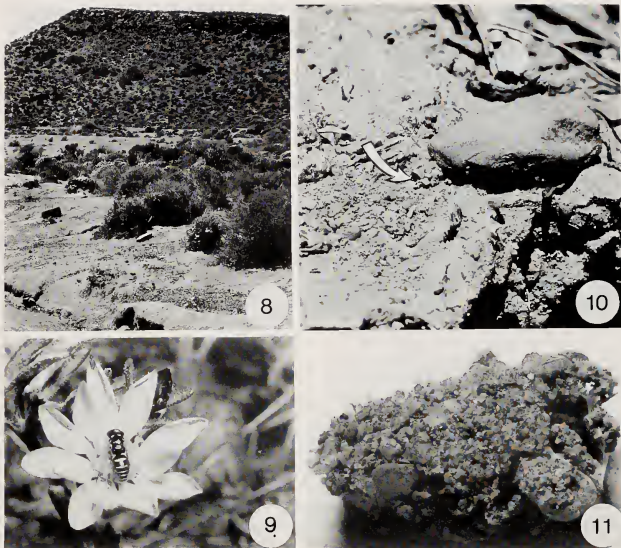
A nesting area of *Q. vagepunctata* was located in the Skuinshoogte Pass (Fig. 8). The vegetation is probably closest to Acocks' Veld Type 28, Western Mountain Karoo (Acocks 1953, 1975). The nesting site was a bare patch of somewhat uneven level ground between shrubs. The soil was sandy and friable.

The site approximately one square metre, was located in October 1989 and revisited in September 1990 when it was again being actively used for nesting.

Plant visiting.— *Quartinia vagepunctata* was foraging almost exclusively on Asteraceae: extremely commonly on flowers of *Relbunium pumila* Thunberg (Fig. 9) in the Skuinshoogte Pass and *Leysera gnaphalodes* (L.) L. in the Goegab Nature Reserve, and at Narap and Anenous; and less commonly on flowers of *Leysera gnaphalodes* above the Nieuwoudtville Waterfall, *Cotula* cf. *leptalea* DC., *Senecio* prob. *niveus* Less., *Pentzia suffruticosa* (L.) Hutch. ex Merxm. and *Osteospermum* cf. *oppositifolia* in the Skuinshoogte Pass, *Pentzia suffruticosa* in the Wildeperdehoek Pass, *Helichrysum* sp. and *Cotula* sp. at Anenous.

The exceptions were a female collected on a low growing *Galenia* sp. (Aizoaceae) growing amongst *Leysera gnaphalodes* at Anenous and a male collected on a flower of *Lebeckia* cf. *sericea* Thunb. (Fabaceae) at Klipfontein. It is of interest that these were visiting flowers of families favoured by other masarines.

The flowers of all but two of these species were yellow. *Senecio* prob. *niveus* has whitish flowers and the *Galenia* sp. pink flowers.



Figs. 8-11. 8, Nesting area of *Quartinia vagepunctata*, Skuinshoogte Pass, 15 km north of Nieuwoudtville on the road to Loeriesfontein. 9, *Quartinia vagepunctata* on flower of *Relbania pumila* (Asteraceae). (approx. $\times 3$). 10, Nesting site of *Quartinia vagepunctata*, arrow indicating sand and silk nest entrance turret. (approx. $\times 1$). 11, Dorsal view of sand and silk nest entrance turret of *Quartinia vagepunctata*. ($\times 14,4$).

Provision.— Provision from four nests of *Quartinia vagepunctata* investigated in the Skuinshoogte Pass was in the form of a relatively moist bright yellow nectar and pollen mass almost entirely filling the cell, adhering to the cell walls and therefore not forming a discrete pollen loaf. The pollen was examined microscopically. That from one nest was of one type only and matched that of *Cotula* and that from the other three nests was of two types mixed and matched that of *Relbania* and *Cotula*.

Description of the nest.— Seven nests of *Q. vagepunctata* were investigated, four on 7.x.1989 and three on 27.ix.1990. Each had its entrance to one side of an earth clod or stone (Fig. 10).

The nest consists of a subterranean silk-lined burrow surmounted by a horizontal turret (Figs 11 and 12), the outer surface of which is of sand (grain

size: 0.16 mm - 1,2 mm) held together by a silk lining. The turret is bag-like, approximately circular in cross-section with its diameter greatest at its outer end and smallest at its inner end. The opening to the burrow entrance is at some little distance from the closed inner end of the bag.

The burrow in the nests investigated consisted of a subvertical shaft, 1,5-2 mm in diameter, terminating in a sealed roughly ovoid cell at depths of 25-30 mm. The cell walls were constructed of sand bonded together with silk and well cemented with an unidentified substance somewhat resinous in appearance. In one of the nests the female was found sheltering in a lateral shaft, suggesting that more than one cell per nest is probably constructed.

Method of construction of the nest.— The soil in which the nest is excavated is friable. Water is not required for nest excavation and is not used as a

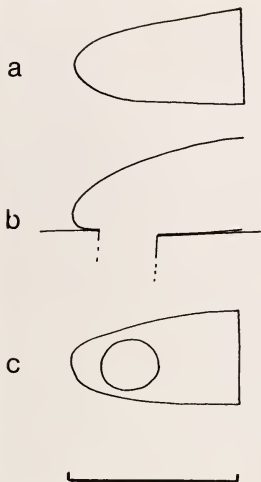


Fig. 12. Plans of turret of *Quartinia vagepunctata*. a. from above; b. vertical section; c. from below. (Scale bar = 5 mm).

bonding agent. It is therefore not surprising that *Q. vagepunctata*, though collected commonly at flowerers, has never been collected at water.

The silk used in nest construction is spun by the nest builder. One individual was observed whilst it was joining together sand grains with silk. It was rotating its head and the silk was apparently issuing from its mouth suggesting that the silk may be produced by mandibular glands.

Male behaviour. — Males, unlike the females, were common on the ground in the vicinity of the forage plants. They were observed to rise up and mount females visiting these plants.

Males were also present at the nesting site.

Associated insects. — Several individuals of *Allocoelia moscaryi* (Brauns) (Chrysididae) were present in close proximity to the nests. As this chrysidid has in addition been found by the authors in association with three *Quartinioides* species and as all known *Allocoelia* associations are with masarines (Kimsey and Bohart 1990) it is suggested that this wasp is most probably a nest parasite of *Quartinia* and *Quartinioides*.

DISCUSSION

Richards (1962) saw the family Masaridae as constituted of three sub-families, the Euparagiinae, Gayellinae and Masarinae, and to be a "sister group" of the families Eumenidae and Vespidae in a superfamily the Vespoidea. Carpenter (1982) assessed the phylogenetic relationships of the components of the Vespoidea (*sensu* Richards) using cladistic methods. He treated Richards' Vespoidea as a single family Vespidae in which he recognized six sub-families, Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Polistinae and Vespinae. He thereby disassociated the Euparagiinae which provision with beetle larvae from Richards' Gayellinae and Masarinae which provision with pollen and nectar. At the same time he associated more closely the Gayellinae (*sensu* Giordani Soika 1974) and Masarinae (*sensu* Richards 1962) by placing them together as tribes (Gayellini and Masarini) in his subfamily Masarinae. Following this grouping the present authors have excluded the Euparagiinae from their discussion. *Ceramius*, the most studied genus, is divided into species groups following Richards (1962) amended by Gess and Gess (1986, 1990).

In order that the nesting accounts for *Celonites latitarsis*, *Celonites wahlenbergiae* and *Quartinia vagepunctata* should be put into context, nesting by the Masarinae (*sensu* Carpenter 1982) as a whole is outlined and discussed.

Basic nest types. — From a review of the published and present accounts of the nesting of the Masarinae it is possible to recognize seven basic nest types:

Nest type 1: a multicellular sub-vertical burrow in horizontal to sub-horizontal ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow but with the excavated cells not containing constructed cells:

Four species of *Ceramius*: all species of Group 8 - *C. capicola* Brauns and *C. linearis* Klug (Gess and Gess 1980), *C. bicolor* (Thunberg) (Gess and Gess 1986) and *C. socius* Turner (Gess and Gess 1988b).

Nest type 2: a multicellular sub-horizontal burrow in vertical to sub-vertical ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow, and with the walls of each excavated cell lined with cemented earth excavated within the burrow:

One species of *Masarina*: *M. familiaris* Richards (Gess and Gess 1988a).

Nest type 3: a multicellular sub-vertical burrow in horizontal to sub-horizontal ground excavated by the nester, with or without an entrance turret constructed from earth extracted from within the burrow, and with each excavated cell containing a constructed cell formed from earth excavated within the burrow:

Three species of *Paragia*: *P. (Paragia) tricolor* Smith (Houston 1984); *P. (Paragia) decipiens* Shuckard (Naumann and Cardale 1987); and *P. (Cygnea) vespiformis* Smith (Houston 1986).

Eleven species of *Ceramius*: Group 2a — *C. cerceiformis* Saussure (Gess and Gess 1988b); Group 2b — *C. clypeatus* Richards (Gess and Gess 1990); Group uncertain, probably 2b — *C. micheneri* (Gess and Gess 1990); all species of Group 3 — *C. nigripennis* Saussure (Gess and Gess 1986), *C. jacoti* Richards (Gess and Gess 1988b), *C. braunsi* Turner and *C. toriger* Schulthess (Gess and Gess 1990); the single species of Group 5 — *C. lichtensteinii* (Klug) (Gess and Gess 1980); Group 6 — *C. rex* Saussure (Gess and Gess 1988b) and *C. metanotalis* Richards (Gess and Gess unpublished fieldnotes); Group 7 — *C. tuberculifer* Saussure (Giraud 1871, Ferton 1901).

Two species of *Jugurtia*: *J. confusa* Richards (Gess and Gess 1980) and *J. braunsi* (Schulthess) (Gess and Gess unpublished field notes).

Nest type 4: a group of constructed earthen cells attached to plant stems or stones:

Six species of *Celonites*: *C. abbreviatus* (Villers) (Lichtenstein 1869 (as *C. apiformis* Fabricius), Ferton 1901, 1910, Bellmann 1984); *C. fischeri* Spinola (Bingham 1898 as reported in Richards 1962); *C. mayeti* Richards (Lichtenstein 1875, Ed. André 1884 as reported in Richards 1962); *C. jousseaumei* du Buysson (Richards 1962); and *C. andrei* Brauns (Brauns 1913); and in addition a putative nest of *C. promontorii* (Brauns) (Gess and Gess 1989).

Eight species of *Pseudomasaris*: *P. coquillei* Rohwer (Richards 1963b); *P. edwardsii* (Cresson) (Torchio 1970); *P. maculifrons* (Fox) (Parker 1967); *P. occidentalis* (Cresson) (Hungerford 1937 as reported in Torchio 1970); *P. phaceliae* Rohwer (Parker 1967, Torchio 1970); *P. texanus* (Cresson) (Bequaert 1940 as reported in Torchio 1970); *P. vespoides* (Cresson) (Torchio 1970); and *P. zonalis* (Cresson) (Parker 1967).

One species of *Gayella*: *G. eumenoides* Spinola (Claude-Joseph 1930 as reported in Richards 1962).

Nest type 5: constructed earthen cells located in a pre-existing cavity; soil for cell construction collected from a quarry site at some distance from the nest:

One species of *Celonites*: *C. wahlenbergiae* (present paper).

Nest type 6: a self-excavated sloping burrow in friable soil with an excavated cell in which is an earthen cell constructed from soil collected from a quarry site at some distance from the nest:

One species of *Celonites*: *C. latitarsis* (present paper).

Nest type 7: a sub-vertical burrow in friable soil, surmounted by a sand and silk turret and having an excavated cell in which is a constructed sand and silk cell:

One species of *Quartinia*: *Q. vagepunctata* (present paper).

Ground nesting has been recorded for a further eleven species, however, the observations are too incomplete for these species to be attributed to the nest types as set out above: (*Paragia* (*Paragia*) *smithii* Saussure (Wilson 1869); *Rolandia maculata* (Meade-Waldo) and an undescribed species of *Riekia* (Houston 1984); *Ceramioipsis paraguayensis* Bertoni (almost certainly a synonym of *C. gestroi* Zavattari (Richards 1962)) (Bertoni 1922 as reported in Richards 1962); three species of *Ceramius*, Group 1 — *C. fonscolombi* Latreille (Fonscolombe 1835), Group 7 — *C. bischoffi* Richards (Richards 1963a), and Group 4 — *C. beyeri* Brauns (Brauns 1910, Gess and Gess 1988b); two species of *Trimeria*, *T. howardi* Bertoni (Zucchi et al. 1976 as reported in Houston 1984) and *T. buyssoni* Brethes (Neff and Simpson 1985); *Quartinia* sp. (Jacot Guillarmod personal communication), and *Quartinoides* sp. (Gess and Gess 1988a, 1989). Conflicting accounts have been given for *Masaris vespiformis* Fabricius. Morice (1900) suggested that this species is ground nesting and Ferton (1920) that it makes aerial mud cells.

Dorr and Neff (1982) described a nest in a beetle boring. The nest consisted of a linear series of four unlined cells separated by mud partitions. This they alleged to be a nest of *Pseudomasaris marginalis* (Cresson), however, confirmation is required.

Bonding agent.— Three bonding agents, water, nectar, and silk, are known to be used by masarines in nest construction.

Use of water in excavation and as the bonding agent is either stated or implied in all nesting accounts of Nest types 1, 2 and 3. In addition the inner surfaces of the cells of *Paragia* (*P.*) *tricolor* are

polished and waterproofed with an unidentified substance (Houston 1984).

Nectar is the proven bonding agent employed by *Pseudomasaris edwardsii* of Nest type 4 (Torchio 1970). Circumstantial evidence, available to the present authors, furthermore suggests that nectar is used by *Celonites* of Nest types 4, 5 and 6.

The use of self-generated silk sets Nest type 7 as exemplified by *Q. vagepunctata* apart from all the others. The use of silk in nest building by wasps seems to be altogether uncommon. It has been noted for two eumenines, one ground nesting (Gess and Gess unpublished fieldnotes) and one nesting in pre-existing cavities (Weaving personal communication), and has been recorded for two social sphecids, one constructing aerial nests, *Microstigmus comes* Krombein (Myers 1934, Matthews and Starr 1984) and one nesting in pre-existing cavities, *Arpactophilus mimi* Naumann (Matthews and Naumann 1988). In both sphecids the adult wasps secrete the silk from glands near the tip of the metasoma. Adult *Q. vagepunctata* observed appeared to produce silk from their mouths and it is suggested therefore that silk is most probably produced by the mandibular glands.

Using nectar or silk as a bonding agent frees the user from dependence on water, an often ephemeral resource in arid areas. The use of silk furthermore makes it possible for the users to construct nests in and with friable soil which otherwise becomes readily unstable under dry conditions.

Method of nest construction by ground nesters.—In the first three nest types water is carried from a water source in the crop. On arrival at the nest it is regurgitated and worked into the soil with the mandibles to form mud. The spoils of excavation are removed with the mandibles in the form of mud pellets which are either discarded, used for the construction of a turret or for the construction of cells.

In the sixth nest type exemplified by *C. latitarsis*, in which the burrow is excavated in friable soil, water is not used and the spoils of excavation are raked out and accumulate to form a tumulus. This is of particular note when the structure of the fore tarsi of *C. latitarsis* is compared with that of ten other Afrotropical species of *Celonites* (Gess 1992). Of those species compared, only *C. latitarsis* has widely expanded tarsomeres suitable for raking soil which suggests that its nest type may be unusual for *Celonites*.

Sand raking seems to be unusual not only for

masarines but for Vespidae as a whole. Furthermore it seems that nesting in friable soil in the Vespidae is probably derived rather than primitive as in the Pompilidae and Sphecidae. Apart from *C. latitarsis* none of those species known to excavate nests in friable soil has fore tarsal sand rakes as possessed by many ground nesting Sphecidae and Pompilidae. Soil removal is effected by the mandibles as in those species excavating in non-friable soil. For example *Pseudepipona herrichii* (Saussure), a eumenine nesting in a vertical burrow in friable ground, removes sand particles with the mandibles one at a time (Spooner 1934 as in Spradbery 1973). The only recorded morphological modification for sand removal is that of the mouthparts of *Pteroecheilus* (Bohart 1940) for which nesting in vertical burrows in friable soil by two species has been recorded (Isely 1914, Evans 1956). Amongst the masarines turretless inclined burrows excavated in sandy ground have been recorded for an undescribed species of *Riekia* and for *Rolandia maculata* (Houston 1984). Unfortunately the method of excavation was not noted and the nests were incomplete.

Not only is the substrate and the method of excavation of the burrows of Nest type 6 very different in nature from that of Nest type 3 but, as importantly, so is the nature of and method of construction of the cells. Whereas the earthen cells of Nest type 3 are constructed from soil quarried within the burrow and bonded with water those of Nest type 6 are constructed from soil quarried at some distance from the burrow and bonded not with water but most probably with nectar. The method of construction and nature of the earthen cells of Nest type 6 as exemplified by *C. latitarsis* in no way differs from that of Nest type 5 as exemplified by *C. wahlenbergiae* nesting in pre-existing burrows and that of Nest type 4 as exemplified by the aerial nesting *Celonites* species.

Evolutionary sequence.—A possible sequence is discernable within the Masarinae from excavated burrows with excavated cells only (Nest type 1) through excavated burrows with constructed earthen cells within excavated cells with earth for construction being derived from within the burrow (Nest type 3) to the presumably more advanced construction of aerial earthen cells (Nest type 4) (discussed in Gess and Gess 1980).

A further possible sequence within the genus *Celonites* is here suggested, that is a return to the ground from aerial earthen cells (Nest type 4)

through constructed earthen cells in pre-existing cavities in the ground (Nest type 5) to self excavated burrows with constructed earthen cells within excavated cells with earth for construction being mined outside the burrow (Nest type 6).

This second sequence is suggested by the method of construction of Nest type 6, notably the sand raking behaviour with the consequent possession of sand-rakes as yet not recorded for any other masarines, soil for cell construction being obtained from a site at some distance from the nest not from within the nest, and the bonding agent being nectar as used in Nest type 4 and 5 not water as is used in Nest type 3.

Nest type 7 is distinct and is possibly derived from a vertical burrow excavated in stable friable soil without the use of a bonding agent.

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The Genus *Oxybelus* in Chile (Hymenoptera: Sphecidae, Crabroninae)

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Abstract.—The large crabronine genus *Oxybelus* contains 9 species in Chile, 8 of them apparently endemic. Descriptions are given of all 9 species, of which 4 (*mimeticus*, *penai*, *tarapacae*, *toroi*) are described as new. Illustrations of the critical features of the metanotum (squamae) and propodeum (mucro) are given.

Oxybelus Latreille is the largest genus in the Crabroninae. It occurs worldwide except for the Australian area. Of the more than 200 listed species (Bohart and Menke 1976), 23 have been recorded from the Neotropical Region.

Recognition of *Oxybelus* depends upon the somewhat winglike protuberances (squamae) of the metanotum, median spear or blade (mucro) of the propodeum, median longitudinal carina of the scutellum and metanotum, and fused submarginal and discoidal cells of the forewing.

Technical symbols used in the key and descriptions are: MOD, median ocellar diameter; LID, least interocular distance; F-I, II, etc., flagellomeres; T-I, II, etc., abdominal terga after the propodeum; squamae and mucro, described above.

Curators and museums (locality symbols in capitals) who have furnished considerable Chilean material or critical types are as follows: J. Genise, Argentine National Museum (BUENOS AIRES); L. Kimsey, University of California Bohart Museum (DAVIS); C. Vardy, British Museum (LONDON); J. Rosen, American Museum of Natural History (NEW YORK); W. Pulawski, California Academy of Sciences (SAN FRANCISCO); L. Stange, Florida State Collection of Arthropods (GAINESVILLE); M. Fritz, Instituto de Investigaciones Entomologicas, Salta, Argentina (SALTA); H. Toro, Universidad Catolica Museum, Chile (VALPARAISO); M. Fischer, Vienna Museum (VIENNA); R. Brooks, University of Kansas Snow Museum (LAWRENCE); A. Menke, U.S. National Museum (WASHINGTON); A. Roland, Universita di Torino, Italy (TURIN). A majority of the specimens were furnished by Haroldo Toro (above).

Systematics.—A short discussion of species characters will help put the Chilean fauna in perspective. Eight of its 9 known species are endemic. One, *joergenseni*, is a wide-ranging South American form which has presumably penetrated a mountain pass to the west. Not only is this species rare in Chile, it is the only one in which the male has a bearded clypeus and three teeth along the median third of the free edge (Fig. 13). This is a situation common among non-Chilean males.

A species character of special value is the sculpturing of the mesopleuron. Females of many South American species have the mesopleuron extensively polished. In males this feature is represented by coarse and widely spaced punctures on an otherwise smooth surface. Many other species have the mesopleuron with moderate and rather close punctation. None of the Chilean forms have the polished condition. However, *chilensis* and *mimeticus* have the mesopleuron rough, and *penai* has vertical ridges. Since no species of *Oxybelus* are known from Australia, no comparison with the Chilean fauna can be made.

In coloration the South American species divide fairly evenly on the basis of red versus all-black on the female pygidial plate or male last tergum. All known Chilean species fall in the red category. In another character based on markings, the reddish tegula and post-tegula (basal wing sclerite) occur in many South American forms. All Chilean species have this situation except *clandestinus*.

Except for *joergenseni* the Chilean species have the pronotal ridge black, a condition rare in other South American forms.

The shape of the metanotal squamae and the following propodeal mucro are important charac-

ters throughout the genus. Among American species the squamae can be divided as follows: (1) slender and pointed (Fig. 8), (2) stout with an apicolateral point (Fig. 4), or (3) long oval with the point obscure (Fig. 1). Of course, there are variations of these. In the Chilean fauna, category (1) contains *clandestinus*, *toroi*, *marginellus*, and

tarapacae; category (2) has *penai*, *mimeticus* and *chilensis*; category (3) includes *joergenseni* and *cordatus*. With respect to the mucro, those in squamal category (1) have it slender, those in (2) have it stout, and those in (3) have it expanded medially or apically.

KEY TO THE CHILEAN SPECIES OF *OXYBELUS*

1. Mucro spiniform or narrow, (Fig. 6), maximum breadth not more than 1.5 MOD; squama narrow, plainly pointed posteriorly or quite small 2
- Mucro relatively broad, at least in female (Fig. 3), maximum breadth more than 2 MOD; squama rounded, subtriangular or long oval 5
2. Squama small but posterior point strong (Figs. 6, 7), midtibia with a basal yellow dot or spot 3
- Squama exceptionally small (Figs. 8, 9), midtibia various 4
3. Tegula and post-tegula brown and white, last tergum red on apical half; terga with close but weakly impressed punctation, somewhat shiny *clandestinus* Kohl
- Tegula and post-tegula red, last 2 or 3 terga red; terga with close, dull punctation *marginellus* Spinola
4. T-I-II with large, separated spots (Fig. 14), other terga with fragmentary yellow; prepectus areolate or with coarse longitudinal ridging; mucro slender but not spinelike (Fig. 8); midtibia all dark *tarapacae* R. Bohart
- Terga with narrow yellow bands, usually on T-I to IV or V; prepectus (below pronotal lobe) punctate; mucro spinelike (Fig. 9); midtibia maculate *toroi* R. Bohart
5. Mucro flattened and expanded (Figs. 1, 2), squamal point lateral and largely concealed; mesopleuron punctate, not unusually coarse 6
- Mucro stout, incurved beneath (Figs. 3 to 5); squamae various; mesopleural sculpture relatively coarse 7
6. Mucro with greatest expansion subapical (Fig. 1), male clypeus with free edge not tridentate, no bearded area above (Fig. 12) *cordatus* Spinola
- Mucro with greatest expansion median (Fig. 2), male clypeus with free edge tridentate below a bearded area (Fig. 13) *joergenseni* Brèthes
7. Squama with posterior point strong (Fig. 4); prepectus with exceptionally coarse, close punctation; T-I to IV all dark or sometimes T-I with lateral yellow spots, rarely T-II also *mimeticus* R. Bohart
- Squama with point weak and lateral or at most slightly exceeding inner lobe (Figs. 3, 5); prepectus moderately punctate or vertically multiridged; T-II, at least, with bright yellow lateral spots 8
8. Lower mesopleuron with coarse punctation but no appressed silvery hair, female with little silvery hair on gena and forefemur; midtibia all dark; mesopleuron without vertical microridging *chilensis* Reed
- Lower mesopleuron moderately punctate but with considerable silvery hair in both sexes, female with much silvery hair on gena and forefemur; midtibia with basal yellow dot; mesopleuron with vertical microridging which is most obvious in female *penai* R. Bohart

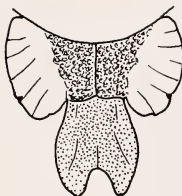
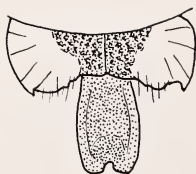
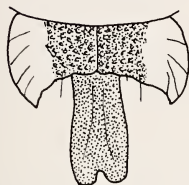
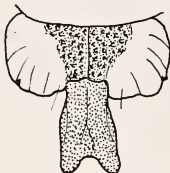
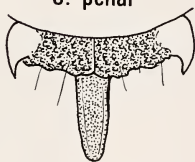
Oxybelus chilensis Reed

Oxybelus chilensis Reed 1894:651. Lectotype male (here designated), Chile (VIENNA).

Oxybelus comatus Reed 1894:651. Chile. Types lost? New synonymy.

Female.— Length 6 mm. Black, tegula, post-tegula, T-VI or V-VI, red; metanotal squamae, subapical bands on T-I to V, those on I to IV separated medially, yellow; eyes brown; wings lightly stained.

Pubescence silvery appressed on face below and pale erect above and on vertex; moderately abundant and silvery on gena, notum, forefemur, lower mesopleuron, and tergal apices. Punctuation moderate and close on head, notum, and terga; coarse on lower mesopleuron; propodeum cross-ridged laterally, ridged to areolate posteriorly. Clypeus with a bevel, flanked by a stout tooth. LID 1.6x eye breadth; metanotal squama rather broad, point lateral; propodeal mucro strong, incurved beneath,

1. *cordatus*2. *joergenseni*3. *chilensis*4. *mimeticus*5. *penai*6. *clandestinus*7. *marginellus*8. *tarapacae*9. *toroi*10. *mimeticus*12. *cordatus*11. *tarapacae*13. *joergenseni*14. *tarapacae*

Figs. 1-9, Squamae and mucro, females. Figs. 10, 11, Femorotibial area, outer view, females. Figs. 12, 13, Clypeus, males; 13a, White beard. Fig. 14, Terga, female, dorsal. Figs. 4, 5, 8, 9, 10, 11, 14, Holotypes. Fig. 12, Paratype. Figs. not drawn to scale.

notched apically (Fig. 3); hindfemur with a strong apicodorsal crest (as in Fig. 10); pygidial plate angled about as in Fig. 14.

Male.—Length 4.5–6 mm. T-VI–VII or V to VII red; T-II to VI with lateral teeth.

Distribution.—The 12 males and 11 females that I have seen are from the Chilean provinces of Coquimbo: Rivadavia, Las Breas; Valparaíso: Las Peñas, Salinas; Santiago: Santiago, Las Condes, El Canelo; Colchagua: Camino a Termas del Flaco; Concepción; Malleco: Lago Icalma, La Fusta Mts., Lago Galletue.

Systematics.—*Oxybelus chilensis* is one of the more abundant species in central Chile. The brown eyes; nearly all black mesonotum; red tegula, post-tegula, and terminal terga; and stout but not expanded mucro are found also in *mimeticus* and *penai*. *O. chilensis* differs from the former species by its more laterally pointed squamae, more extensive tergal maculation, and all dark male midtibia. The coarse vertical ridging of the mesopleuron and extensive silvery pubescence are distinctive in *penai* and will separate it from *chilensis*. Both sexes of *penai* have the lower mesopleuron with silvery hair. In *chilensis* this area is coarsely punctate and not silvery appressed. The poorly described type of *comatus* has not been located and may be lost. The synonymy of *comatus* is based on a specimen of *chilensis* in the British Museum determined by Reed as *comatus*.

Oxybelus clandestinus Kohl

Oxybelus clandestinus Kohl 1905:358. Lectotype female (here designated), Concepcion, Concepcion Prov., Chile (VIENNA).

Female.—Length 6 mm. Black, antenna beneath and apically, mandible medially, pygidial plate apically, reddish; mandible to near base, tegula, post-tegula in part, tibiae basally (extended on foretibia), squama, apicolateral streaks on T-I–II (broken medially) pale yellow; eyes gray; wings very lightly stained. Pubescence silvery appressed on lower half of face, gena, mesopleuron (weak), tergal apices, and pygidial plate. Punctuation mostly fine and close, a little more coarse on mesopleuron; propodeum with cross-ridging laterally and posterolaterally, broadly areolate toward base below metanotum. Free clypeal margin nearly straight, not beveled, a tooth at outer fifth, a small knob on clypeus medially; LID 1.2x eye breadth;

metanotal squamae small, posteriorly pointed, broadly disconnected; propodeal mucro narrow, tapering to a slightly rounded apex (Fig. 6); pygidial plate angled about as in Fig. 14.

Male.—Length 5 mm. No lateral tergal teeth, LID 1.1x eye breadth, T-I only with lateral streak or all T-I to VI dark, T-VII reddish on apical half.

Distribution.—I have seen 7 males and 2 females from the following Chilean Provinces: Nuble: Termas de Chillan, I-27-67 (M. E. Irwin), Concepción (type female and male). Malleco: La Fusta Mts., II-21-62 (L. E. Peña); Curacautin 3 km.s., I-14-89 (L. S. Kimsey).

Systematics.—The slender mucro, pointed squamae, mostly dark tegula and post-tegula, red apical half of last tergum, and gray eyes of museum specimens are characteristic.

Oxybelus cordatus Spinola

Oxybelus cordatus Spinola 1851: 364. Lectotype female (here designated), Chile: "provincias del norte, en Coquimbo, etc." (TURIN).

Female.—Length 4–5 mm. Black, apical two-thirds of flagellum, tegula, post-tegula, legs partly, T-V usually, T-VII, reddish; mandible to base, pronotal lobe, squama, mucro around edge, femora toward apex, tibiae outwardly, lateral spots on T-I, lateral subapical streaks on T-II to IV, pale yellow; eyes gray, wings lightly stained. Pubescence silvery appressed on lower face, becoming yellowish above and brownish on vertex where it is erect but short; off-silvery hair on notum; silvery appressed on gena, mesopleuron, and tergal apices; pygidial setae yellowish. Punctuation fine and close, propodeum mostly polished laterally, weakly sculptured posteriorly. Clypeus with free edge beveled across middle half, flanked by a sharp tooth, median knob obsolete; LID about equal to eye breadth; metanotal squama broad, point lateral; propodeal mucro flattened, about as broad as long, obtusely notched at apex (Fig. 1); hindfemur with a moderate apicodorsal crest; pygidial plate angled at 75°, unusually narrow at apex.

Male.—Length 4–5 mm. Last flagellomere black, T-V to VII usually red, legs more extensively yellow, mucro usually a little more narrow, T-II to VI with small lateral teeth, clypeal shape (Fig. 12). Distribution. This is the most abundant and widely dispersed of the Chilean *Oxybelus*. I have studied about 320 males and 120 females from the follow-

ing Chilean Provinces: Atacama, Coquimbo, Aconcagua, Valparaíso, Santiago, O'Higgins, Curico, Linares, Nuble, Bio-Bio, Malleco, and Aisen.

Systematics.— Principal characters are the extensive yellow leg markings, flat mucro which is short and broad as well as obtusely notched apically (Fig. 1), relatively simple male clypeus, and overall fine punctation.

Oxybelus joergenseni Brèthes

Oxybelus joergenseni Brèthes 1913: 141. Holotype female (Type examined), Mendoza, Mendoza Prov., Argentina (BUENOS AIRES).

Female.—Length 7 mm. Black, flagellum clypeal bevel, tegula, post-tegula, legs slightly, T-V-VI and associated sterna, red; mandible mostly, pronotum nearly all across, subapical spots, squamae, apical femoral spots, subapical bands on T-I to IV, that on I enlarged laterally, yellow; eyes gray; wings nearly clear. Pubescence silvery appressed on lower face, gena, forefemur, mesopleuron; off-silvery on vertex, notum. Punctuation moderately fine and close on vertex, notum; moderate and somewhat separated on shiny integument of upper face, mesopleuron; fine and close on terga, propodeum mostly polished laterally, weakly areolate posteriorly. Clypeus with free edge beveled across middle three-fifths, flanked by a sharp tooth, median knob present; LID about equal to eye breadth; metanotal squama longer than broad, point latera; mucro flattened, expanded medially, acutely notched at apex (Fig. 2); hind femur with strong apicodorsal crest; pygidial plate angled at about 80°; sides distinctly convex.

Male.—Length about 5 mm. Last flagellomere dark, T-VI-VII red, tibiae and tarsi extensively yellow, free edge of clypeus with 3 teeth medially (Fig. 13), central one dividing a beard, T-III to VI with slender lateral teeth.

Distribution.— *Oxybelus joergenseni* occurs widely in South America. The only Chilean material I have seen are 2 males from the U.S. National Museum. Data on the specimens are "Chile, R. C. Shannon."

Systematics.— Characteristics of this species are the expanded mucro, convexly sided female pygidial plate, red T-V-VI (female) or T-V to VII (male), tridentate male clypeus, red tegula and post-tegula, and complete yellow bands on T-I to IV. In addition it differs from other Chilean species by having pale markings on the pronotal ridge.

Oxybelus marginellus Spinola

Oxybelus marginellus Spinola 1851: 365. Lectotype male (here designated), Chile (TURIN).

Female.—Length 6.0-6.5 mm. Black, antenna weakly beneath, tegula and post-tegula, T-V at least partly, and pygidial plate, red; squama, basal tibial spots, lateral spots on T-I-II, lateral streaks on T-IV or absent, pale yellow; eyes usually brown; wings very lightly stained. Pubescence silvery appressed on lower face, gena, and apical bands of T-I to IV; brownish erect hair on upper face, vertex, notum, and mesopleuron; golden are apical fringe of T-V and sparse setae of pygidial plate. Punctuation rather fine to moderate, a few larger punctures on mesopleuron above and on rather polished lower area; propodeum cross-ridged laterally, areolate posteriorly. Free clypeal margin toothed at lateral fourth, flanking a median beveled strip, a small knob on clypeus medially; LID 1.2x eye breadth, metanotal squama small, pointed; propodeal mucro clublike, gradually expanding to 1 MOD with hardly incised apex (Fig. 7); hind femur without a prominent apicodorsal crest; pygidial plate angled about as in Fig. 14.

Male.—Length 4.5-5 mm. Lateral teeth weakly developed on T-III to VI; erect hair on upper face, vertex, and mesopleuron pale; T-V to VII red; mandible sometimes partly yellow.

Distribution.— Thirteen males, 4 females, from Chilean Provinces: Aconcagua: Los Riecello, 2800 meters, I-20-74 (H. Toro); Santiago: Santiago (A. Faz), Las Condes, X-1953 (L. Peña) Cañon del Plomo, XII-1988 (M. Fritz); Nuble: Termas de Chillan, I-27-67 (M. Irwin); Malleco: Lago Icalma, I-15-62 (L. Peña), I-II-79 (O. Martinez), I-II-79 (Pasten), I-12-89 (L. Kimsey), Lago Galletue, I-9-62 (L. Peña).

Systematics.— The usually brown eyes of museum specimens, slender but not spinelike mucro, basal tibial spots, red tegula and post-tegula, and brownish erect hair of the female upper face and vertex, characterize the species.

Oxybelus mimeticus R. Bohart, new species

Female holotype.—Length 7 mm. Black, tegula posteriorly, post-tegula inwardly, T-V-VI (VI yellowish), red; metanotal squama on outer half, weak basolateral dot on T-I, yellow; eyes mahogany red; wings nearly clear, venation dark brown. Facial pubescence silvery appressed below, erect and

partly brownish above, pale on thorax (not appressed on mesopleuron), and laterally (not fringed) on terga. Punctuation moderate and close on head, notum and terga, quite coarse and about 0.5 MOD on mesopleuron; genal area multiridged; propodeum partly cross-ridged laterally, coarsely posterolaterally and behind metanotum. Clypeus with a weakly impressed bevel, flanked by a stout tooth; LID much greater than eye breadth; metanotal squama with point posterior; propodeal mucus strong, twice as long as broad, incurved beneath, with a small apical notch (Fig. 4); hindfemur with a stout apicodorsal crest (Fig. 10); pygidial plate angled about as in Fig. 14.

Male.—Length 5.5–6.0 mm. About as in female; LID about 1.3x eye breadth, T-I sometimes all black, midtibia and hindtibia sometimes with basal yellow dots, T-V to VII and associated sterna red; lateral teeth on T-II to VI well developed.

Types.—Holotype female (American Museum of Natural History, NEW YORK), Chile, Atacama: 26 mi. s. Copiapó, X-19-69 (J. Rozen, L. Peña). Paratypes, 16 males, 2 females, Chilean Provinces: Atacama: Rio Pinte, 1400 m, II-2-67 (L. Peña, VALPARAISO); Paipote, X-12-71 (J. Rozen, L. Peña, NEW YORK); Tierra Amarilla, II-1-72 (W. Sielfeld, H. Toro, VALPARAISO); Los Loros, X-4-82 (E. Chiappa, DAVIS). Coquimbo: Las Breas, XI-78 (H. Toro, DAVIS); Balala, X-18-79 (L. Ruz), VALPARAISO; 5 mi. n. Laguna Dam, 8000 ft., XII-6-50 (E. Ross, A. Michelbacher, SAN FRANCISCO), Rivadavia, X-29-57 (L. Peña, VALPARAISO). Santiago: Rio Clarillo, Cordillera, XII-1989 (L. Stange, GAINESVILLE).

Systematics.—The stout and downcurved mucus occurs in *penai*, *mimeticus*, and *chilensis*. All of these have the mesopleural punctuation close and rough. However, the first two have it exceptionally rough, and *penai* has vertical ridges and abundant silvery hair on the lower mesopleuron in addition. The squamae of *mimeticus* are moderately stout but have a strong posterior point. In the other two, the squamae are broader and the point is more lateral.

Oxybelus penai R. Bohart, new species

Female holotype.—Length 7 mm. Black, tegula, post-tegula, T-V-VI, red (pygidium only a little brown-tinged in a female paratype); pronotal lobe dully, basal dots on midtibia and hindtibia, lateral spots on T-I to IV, yellow; eyes brown; wings nearly clear. Appressed facial pubescence silvery,

erect hair above pale but a little dark on vertex (much darker in paratypes); abundant, rather appressed, somewhat shaggy silvery hair on gena, femora, and lower mesopleuron; pygidial setae pale golden. Punctuation moderate and close on head, notum and terga; multiridging on gena (obscured by pubescence); mesopleuron with prominent dorsoventral multiridging; propodeum with strong lengthwise ridges laterally, cross-ridges posteriorly. Clypeus with a pronounced bevel, flanked by a weak tooth, a prominent median knob above; LID 1.6x eye breadth, face bulging toward middle; metanotal squama large, pointed laterally before posterior apex, propodeal mucus strong, twice as long as broad, incurved beneath, with a moderate apical notch (Fig. 5); hindfemur with a moderate apicodorsal crest; pygidial plate angled at 85°.

Male.—Length 6 mm. As in female but silvery pubescence less prominent, T-V to VII red, T-II to VI with lateral teeth.

Types.—Holotype female (Catolica Museum, VALPARAISO), Chile, Valparaiso Province, Concon, II-1963 (Nuñez). Paratypes, 36 males, 7 females, collected by L. Peña, L. Ruz, E. Reed, A. Faz, J. Lagunacelaya, E. Tosti-Croce, F. Rodriguez, H. Toro, and L. Kimsey. Provinces of paratypes are Atacama: La Junta; Coquimbo: Las Breas, Rivadavia; Valparaiso: Las Peñas, Via del Mar, Olmue, Salinas; Santiago: Santiago, El Peumo, Pudahuel, El Canelo; Colchagua: Camino a Termas del Flaco; Curico: Los Quenes, Mt. Tonlema; Talca: El Radal, 1100 m; Linares: Villego; Malleco: Conguillio National Park, Nahuelbuta; Chiloe: Los Quillon. Paratypes have been deposited in the museums listed in the introduction. The species is named for the well-known Chilean collector, Luis E. Peña.

Systematics.—Related species, judging by the similar squamae and mucus, are *mimeticus* and *chilensis*. The vertical multiridging of the mesopleuron is distinctive. However, it may not be easily seen in some males, and there might be confusion with *chilensis*. In these cases the silvering of the lower mesopleuron in *penai* is differentiating. From *mimeticus* the lateral rather than posteriorly pointing squamae of *penai*, as well as the extensive silvery hair of the female, are additional differences.

Oxybelus tarapacae R. Bohart, new species

Female holotype.—Length 6 mm. Black, flagellum toward apex beneath, tarsi dully toward apex, tegula and post-tegula, T-V apically, T-VI and associated sternum, red; large lateral spots on T-I-II, thin and broken subapical line on T-III, yellow (Fig. 14); wings a little stained; eyes brownish grey (brownier in paratypes). Appressed facial pubescences silvery, that of vertex and elsewhere pale and scanty (erect on mesopleuron), pygidial setae reddish golden. Punctuation mostly rather fine and close, mesopleuron with longitudinal ridges, strongest on prepectus, lower mesopleuron moderately punctate, propodeum laterally almost all polished, cross-ridged posterolaterally, areolate below metanotum, terga a little polished between punctures. Clypeus with an obtuse bevel flanked by a small tooth; LID 1.5x eye breadth; metanotal squama small, posteriorly pointed, mucro finger-like, not sharply pointed (Fig. 8); hindfemur without an apicodorsal crest (Fig. 11); pygidial plate angled as in Fig. 14.

Male.—Length 5 mm. T-VI and T-VII mostly red, no lateral tergal teeth.

Types.—Holotype female (Catolica Museum, VALPARAISO), Chile, Tarapaca Prov.: Chusmisa, X-15-81 (H. Burgos). Paratypes (DAVIS), male, female, Tarapaca Prov.: Chusmisa, II-82 (P. Toro).

Systematics.—The dark squama, relatively large yellow spots on T-I-II, and all dark legs, characterize the species.

Oxybelus toroi R. Bohart, new species

Female holotype.—Length 5 mm; black, flagellum and tarsi mostly, tegula, post-tegula inwardly, terga V-VI and associated sterna, red; mandible medially, pronotal lobe, post-tegula outwardly, tibiae outwardly, metanotal squamae weakly, narrow subapical bands on T-I to V, that on V a little reddish, that on I slightly enlarged laterad, yellow; eyes gray; wings nearly clear. Appressed facial pubescence, erect vertex hair, appressed mesopleural pubescence, tergal fringes, pygidial setae, very

slightly off-silvery. Punctuation moderately fine and rather close on head, thorax and terga; propodeum with cross-ridging laterally and posterolaterally, broadly areolate toward base below metanotum. Clypeus with an obtuse median bevel, flanked by a sharp tooth; LID greater than eye breadth; metanotal squamae quite small and widely separated; propodeal mucro a slender spike (Fig. 9); hindfemur without an apicodorsal crest; pygidial plate angled at 85°.

Male.—Length 4.0-4.5 mm. No lateral tergal teeth, LID only a little greater than eye breadth, T-VI-VII red, mandible yellow to near base, tibiae mostly dark.

Types.—Holotype female (Catolica Museum, VALPARAISO), Chile, Antofagasta Prov.: San Pedro, I-7-71 (W. Sielfeld). Paratypes, 4 males, 2 females, same data as type; other paratypes, Antofagasta Prov.: male, Chiu-Chiu, I-24-72 (W. Sielfeld); female, Quillagua, X-12-81 (E. Tosti-Croce); male, Losana, IX-13-71 (L. Ruz); Tarapaca Prov.: Iquique, Quebrada de Chiza, II-II-89 (R. Miller, L. Stange). Paratypes have been deposited in the museums listed in the introduction.

Systematics.—The spinelike mucro (so slender that it may be broken off in some males), tiny squamae (Fig. 9), narrow yellow tergal bands, and gray eyes of museum specimens, are characteristic.

The species is named for Haroldo Toro, who furnished the majority of the specimens used in this study.

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Functional Morphology of the Abdomen and Phylogeny of Chrysidid Wasps (Hymenoptera: Chrysididae)

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Abstract.—The wasp family Chrysididae is characterized in part by the loss of a functional sting, and the internalization of 2 or more abdominal segments. These segments are telescoped within the abdomen and function as an independently muscled ovipositor or genital tube. Accompanying this internalization are shifts in the position of the major muscles involved in pronation, retraction and protraction of the segments from that of the typical ground plan seen in other stinging wasps. There is also an accompanying loss of musculature on the remaining external segments. The degree of modification and internalization correlates with the type of host parasitized, with the least in Cleptinae (parasites of prepupal sawflies), and the most modification in Chrysidinae (nest parasites of bees and wasps). Phylogenetic relationships among chrysidid subfamilies can be traced using derived features of structural and muscular changes in the abdomen. In addition, these modifications reflect compromises between oviposition, copulation and defense.

There are few studies of insects in which attempts are made to explore the function of structural features commonly used in systematics to demonstrate phylogenetic relationships. Within Hymenoptera the structure and function of the ovipositor has been examined in some detail (Austin 1983, Austin and Browning 1981, Copland and King 1971, Oeser 1961, Robertson 1968, Scudder 1961).

Unfortunately, in many insect groups neither the systematics nor the biology are sufficiently well understood to permit the examination of relationships between structural modifications and hosts, or other aspects of the biology. The family Chrysididae is one exception to this problem. The family has just been revised on a world basis, with detailed analysis of phylogenetic relationships (Kimsey and Bohart 1991), and at least general categories of hosts are known for tribes and subfamilies. There appear to be strong correlations in this family between the type of host and modifications of the chrysidid abdomen, in both sexes. These changes in external and internal morphology of the chrysidid abdomen support relationships discussed previously (Bohart and Kimsey 1982, Kimsey and Bohart 1991).

In the vast majority of aculeate, or "stinging", wasps the ovipositor functions as both a defensive and an offensive structure, used to inject prey or potential predators with venom. This sting apparatus has been secondarily lost or highly reduced in several groups, including the stingless bees

(Meliponini, Apidae), a number of ant taxa, and Chrysididae. In all but the last group the apparent abdomen is otherwise relatively unmodified, with 6 external segments in females and 7 in males, excluding the propodeum, and the sting apparatus involves segments VIII and IX. The male genital capsule is internally subtended by gastral segment IX. The structure of the sting and male terminalia have been studied in detail by Carpenter (1986), Oeser (1961), Rasnitsyn (1980) and Snodgrass (1942) among others.

However, within the family Chrysididae radical changes in the abdomen of both males and females have occurred. In this group the sting is considerably reduced and functions more as an egg guide than in any defensive manner, and both the male and female genitalia are subtended by an eversible tube formed by 2 or more internalized abdominal segments.

Somewhere in the transition from some ancestral form to the Chrysididae the 2 apical external abdominal segments (VI and VII in females, and VII and VIII in males) were internalized, resulting in a primitive ground-plan of 5 external segments in males and 4 in females; a condition found in Cleptinae, Amiseginae and Loboscelidiinae. Although this ground-plan of 5 external abdominal segments is primitive for chrysidids, it is apomorphic within the Aculeata. This basic modification of the abdomen in turn facilitated a series of specializations that are unique to this family,

which reflect various compromises between oviposition, copulation and defense.

MATERIALS AND METHODS

This study is based on morphological studies of the family Chrysididae. External morphology of more than 2000 species of Chrysididae was examined for a monograph of the family (Kimsey and Bohart 1991). Internal anatomy was studied in dissections of preserved material representing several aculeate families, and subfamily groupings within the Chrysididae (Table 1).

Table 1. Taxa dissected for studies of abdominal musculature. The sex of specimens examined is given in parentheses, M = male, F = female.

Family	Subfamily	Species
Chrysididae	Chrysidinae	<i>Chrysis nitidula</i> (Fab.) M, F
		<i>Chrysis</i> sp. M
		<i>Chrysirissa densa</i> (Cr.) M, F
		<i>Chrysura</i> sp. (f)
		<i>Hedychrum</i> sp. M, F
	Cleptinae	<i>Cleptes alienus</i> Patton M
		<i>Cleptes semiauratus</i> (L.) F
		<i>Adelphæ anisomorphae</i> Kr. M, F
Bethyilidae	Amiseginae	<i>Rhabdelyris</i> sp. M, F
		<i>Auplopus</i> sp. M
Pompilidae		
Apidae		<i>Apis mellifera</i> L. F

The muscle arrangements found in *Rhabdelyris* (Bethyilidae), *Auplopus* (Pompilidae) and *Apis* (Apidae) all closely resembled one another (as in Fig. 1). Therefore, the condition found in these taxa was used as the primitive ground plan against which the muscle positions in chrysidids were compared (Figs. 2-4).

These specimens were fixed in solutions using formalin-acetic acid (FAA). Unfortunately, I could only obtain specimens of *Adelphæ* and *Rhabdelyris* preserved directly in 70% ethanol, without an interim fixative. The relatively poor state of preservation of these specimens made it impossible to determine muscle attachments in the ultimate and penultimate abdominal segments, those directly involved with the sting and genital capsule.

Although the chrysidid abdomen is quite modified, homologies can be seen between the musculature in this family and that of other aculeates. There have been few published studies of the abdominal musculature of Aculeata (Duncan 1939, Snodgrass 1942). As a result, I am using the terminology for the musculature of Snodgrass (1942) where possible, to aid in comparisons (Table

Table 2. Terminology taken from Snodgrass (1942) and code numbers used in Figs. 1-4 for muscles of the apparent abdomen, beginning at the petiole.

- 1s—*Median Intersegmental Ventral Muscle of Metathorax*. This is the primary depressor of the abdomen, originating on the metasternum and attaching on sternum II (Snodgrass No. 118).
- 2s—*Oblique Internal Ventral Muscle of Segment III*. This muscle originates near the midline of segment III and attaches on the anterior apodeme of segment IV. It was found only in Chrysidinae. There is no clearly homologous muscle in the honeybee or other aculeates. It may be derived from 3s as that muscle has the same point of insertion.
- 3s—*Lateral Internal Ventral Muscle*. This muscle originates adjacent to the anterior sternal apodeme of the anterior sternum, and attaches on anterior apodeme of the posterior sternum (Snodgrass Nos. 131, 142, 153, 164, 175).
- 4s—*Medial Internal Ventral Muscle*. Originates on the apical margin of the anterior sternum, and attaches on anterior margin of the posterior sternum (Snodgrass Nos. 130, 141, 152, 163, 174).
- 5s—*External Ventral Muscle*. This muscle originates basally on the anterior sternum and attaches on the apodeme of the posterior sternum (Snodgrass Nos. 135, 146, 157, 168).
- 1t—*Medial Internal Dorsal Muscle*. This muscle originates posterior to the anterior apodeme of the anterior tergum, and attaches apicomediaally on the posterior tergum (Snodgrass Nos. 124, 133, 144, 155, 166).
- 2t—*Lateral Internal Dorsal Muscle*. This muscle originates posterior to the apodeme of the anterior tergum, and attaches laterally on the posterior tergum (Snodgrass Nos. 125, 134, 145, 156, 167).
- 3t—*External Dorsal Muscle*. This muscle originates posterolaterally on the anterior tergum, and inserts on the anterior apodeme of the posterior tergum (Snodgrass Nos. 135, 146, 157, 168).
- 1ts—*Lateral Muscle of Tergum II*. This muscle originates on the dorsal surface of the tergum, and attaches on the anterior margin of the sternum (Snodgrass No. 129).
- 2ts—*First Lateral Muscle*. This muscle originates posterolaterally on the tergum, and extends apicolaterally between sternum and tergum, attaching below the anterior apodeme of the sternum (Snodgrass Nos. 138, 149, 160, 171).
- 3ts—*Second Lateral Muscle*. This muscle originates laterally on the sternum, and inserts laterally on the tergum (Snodgrass Nos. 13 9, 150, 161, 172).

2). Homologies were determined by the position of the muscle insertions, and the assumption that a shift in position was more likely than derivation of an entirely new muscle. The insertion was assumed to be the narrowest part of the muscle, often with a distinct tendon. This is not always easy to determine in Snodgrass' illustrations.

Phylogenetic analysis of the resulting data set was done with the program Hennig-86 of Farris.

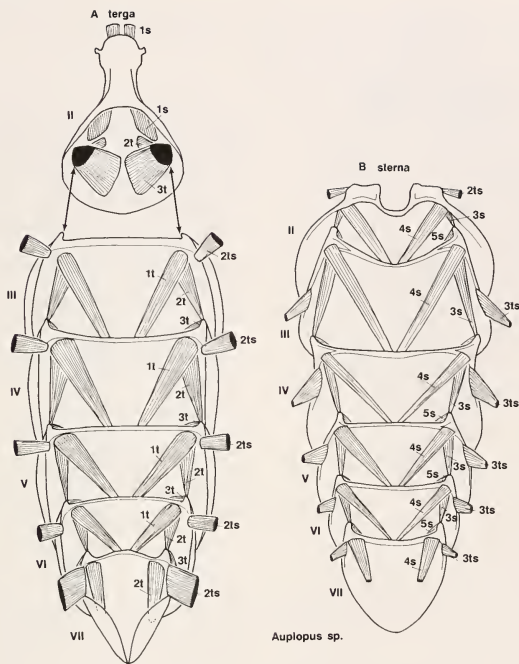


Fig. 1. *Auplopus* sp., male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

RESULTS

Nonchrysidid Abdomen

The abdominal musculature of the external abdominal segments appears to be fairly consistent when comparisons are made among distantly related families. The typical configuration can be seen in Fig. 1. The basic muscle pattern is repeated from one segment to the next, except in the first and last external segments. There are basically 3 sternal, 3 tergal and 3 tergosternal muscle pairs in each intermediate segment. The primary intersegmental muscles, 3s, 4s, 1t and 2t form a V-shaped con-

figuration in the 3 nonchrysidid species examined (as in Fig. 1).

Chrysidid Abdomen

Although homologies can be seen between the musculature of the chrysidid abdomen and that of other aculeates, there are a considerable number of variations in muscle positions and development between the two as well as among the chrysidid subfamilies (Tables 2-3).

The significance of one difference in the musculature of segment II between the Chrysididae and other Aculeata examined is unclear. In other

Table 3. A comparison of the presence or absence of specific muscles in 3 chrysidid subfamilies and the pompilid *Auplopus*. The muscle numbers correspond with those given in Table 2.

Segment No. <i>Auplopus</i> and Muscle		Cleptinae	Amiseginae	Chrysidinae
II	1ts	+	+	+
	2ts	+	0	0
	3ts	0	+	+
	1t	+	+	0
	3t	+	+	+
	3s	+	+	0
III	4s	+	+	+
	5s	+	+	+
	2ts	+	+	0
	3ts	+	+	+
	1t	+	+	+
	2t	+	+	0
IV	3t	+	+	+
	2s	0	0	+
	3s	+	+	+
	4s	+	+	+
	5s	+	+	+
	2ts	+	+	0
V	3ts	+	+	+
	1t	+	+	+
	2t	+	+	0
	3t	+	+	+
	3s	+	+	+
	4s	+	+	0
VI	5s	+	+	+
	2ts	+	+	0
	3ts	+	+	+
	1t	+	+	0
	2t	+	+	0
	3t	+	+	+
VII	3s	+	+	+
	4s	+	+	0
	5s	+	+	+
	2ts	+	+	+
	3ts	+	+	+
VIII	1t	+	+	0
	2t	+	+	+
	3t	+	+	+
	3s	+	+	0
	4s	+	+	0
IX	5s	+	+	+
	2ts	+	+	+

aculeates sternum II has one tergo-sternal muscle pair inserting on the anterior apodeme. Thus it is labeled 2ts in Fig. 1B. In chrysidids there is only one tergo-sternal muscle pair on segment II but since this is located laterally near the middle of the plate it is labeled 3ts. Superficially this appears to be a major difference between the two groups, but in fact may be a shift in the position of 2ts in chrysidids.

Cladistic analysis of the data set generated by muscle traits found in the chrysidid and

nonchrysidid taxa, using the Hennig-86 program of Farris, resulted in a CI of 100 and RI of 100.

MORPHOLOGY

Cleptinae.—The external gastral segments are unspecialized; males have 5 segments and females 4. These external segments are freely articulated and well muscled. The remaining abdominal segments form an ovipositor or genital tube from segments VI-VIII (females) or VII-IX (males), which is held telescoped within the abdomen.

The internal segments VI or VII-IX are not particularly differentiated from the external ones. They differ primarily in the absence of the distinctive lateral tergal lobe seen on the external segments. Terga II-V or VI have a large lateral lobe, the laterotergite, set off from the rest of the tergum by a faint weakening apically and by the position of the spiracle. This lobe covers a large part of the sternum.

Cleptines have largely retained the V-shaped configuration of 1t and 2t, and 3s and 4s, typical of other aculeates (Fig. 2). These 4 muscle pairs are also well developed. However, 1t and 2t have anteriorly shifted away from the anterior apodeme and have assumed a more medial position.

Amiseginae.—As in cleptines the external abdomen consists of 5 segments in males and 4 in females. However, in this group the intersegmental musculature and configuration of the terga has been considerably modified (Fig. 3). The invaginated segments VI or VII-VIII are greatly reduced, with VIII represented by linear, almost membranous flaps. In addition, terga II and III cannot be moved independently and appear to be closely articulated or fused. No indication of the presence of 1t or 2t could be found between these two segments.

There are also other differences on segments III-VI. Muscles 1t and 4s are very slender, and are located nearly parallel with the midline of the plate. 2t and 3s are short and originate away from the anterior apodeme, often toward the midline of the segment.

Unlike the Cleptinae, terga II-IV or V have the laterotergite clearly delimited by a sulcus extending from the anterior to the posterior tergal margin. The spiracle is located just ventrad of this sulcus. This tergal sulcus forms a midline extending the length of the abdomen when it is viewed in profile.

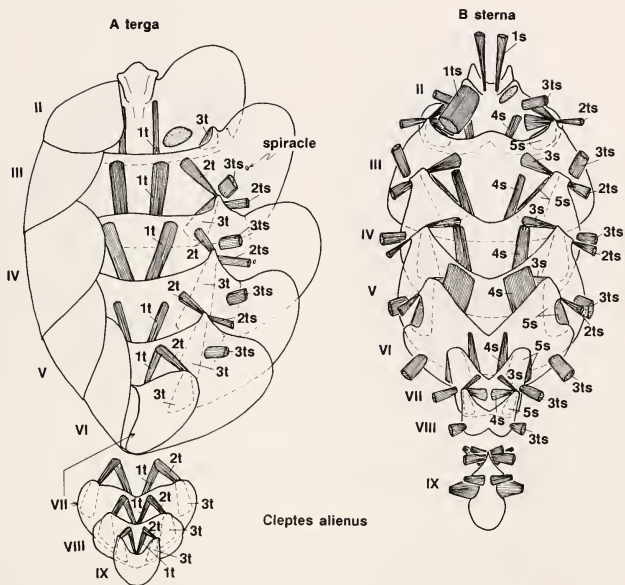


Fig. 2. *Cleptes alienus*, male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

The terga and sterna are both convex in this subfamily.

The reduced internal segments result in a different configuration of the ovipositor and genital tube as compared with other chrysids. In females, segments VI–VIII form a sheath around the elongate sting elements, rather than a separate eversible tube basad of the sting elements. Segments VII–IX are also reduced in males, and form a short, simple pregenital element at the base of the genital capsule.

Based on dissections of dried specimens of *Loboscelidia* (Loboscelidiinae), and the descriptions of Day (1978), the structure of the abdominal terga and sterna are nearly identical to those in Amiseginae. The abdominal musculature in loboscelidiines probably closely resembles that of amisegines.

Chrysidiinae.—The number of external gastral segments is reduced to 4 or fewer in males and 3 or fewer in females, depending on the tribe. Parnopines are the least reduced with 4 in males and 3 in females (Telford 1964). Elampines and chrysidiines have 3 in both sexes, and allocoeliines have 2 in both sexes, with the sternum of segment IV still largely exposed.

The musculature is considerably modified on these external segments (Fig. 4). As in Amiseginae the tergum is sharply divided into a primary tergite and secondary laterotergite by a sulcus. The spiracle may be located near the sulcus on the primary tergite or on the laterotergite. The sterna are narrowed and the laterotergite sharply bent ventrad, forming part of the apparent sternum. The juncture between the primary tergite and laterotergite is

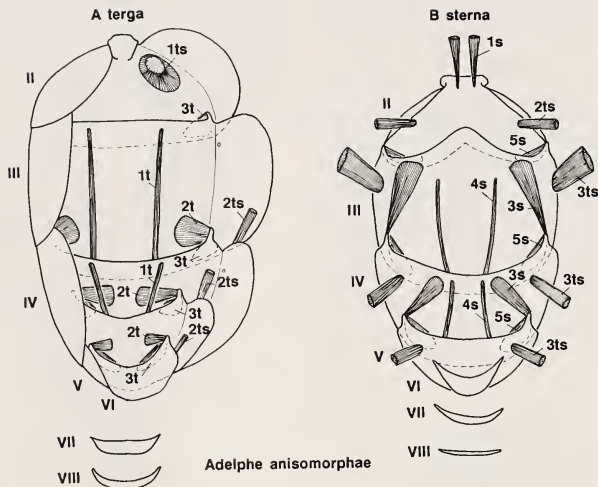


Fig. 3. *Adelpho anisomorphae*, male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

sharply folded. The resulting sternum is flat or concave, giving the gaster a cuplike appearance. The internalized segments are highly modified in chrysidines. However, they have all retained the basic musculature found on these segments in other aculeates.

In addition, chrysidines can roll up in a tight ball when disturbed. Several structural changes allow this posture. The region around the petiolar articulation between the propodeum and first gastral segment has become modified, allowing the abdomen to be rotated up against the thoracic venter. The petiolar socket is broader in chrysidines, the hindcoxal articulations are oriented in a more horizontal position than in cleptines, and the upper surface of the hindcoxae is flattened, allowing the abdomen to rotate anteroventrally and cover the legs and thoracic venter. When the abdomen is curled up against the head and thorax only the top of the eyes, the upper one-third of the thorax and the femorotibial articulations of the legs are visible (Fig. 5b).

The arrangement of muscles in the Chrysidinae

differs considerably from that of other chrysids as well as other aculeates, although it more closely resembles the pattern seen in Amiseginae than any other taxa (Table 3). There are 2 sternal muscles (Fig. 4B) on segments III and IV, which differ in position from that seen in the other taxa examined. These are labeled 4s and 2s respectively. Muscle 4s has a similar attachment and insertion as 4s in other chrysids. Muscle 2s does not appear to be homologous with any muscle seen in the aculeate ground plan, although the insertion of this muscle on the anterolateral apodeme suggests that it may be derived from 3s. However, contraction of both of these muscles would not only pull the sternal plate anteriorly but would also bend the plates involved, increasing the convexity of the abdominal sternum.

There are other differences in musculature as well. Segments III-V lack 2t and 2ts, and segments IV-VI lack 4s. Finally, segment III lacks 2s.

Segment IV is the most highly modified in Chrysidini where the origin of 3t, the primary protractor of the internal segments, is marked by

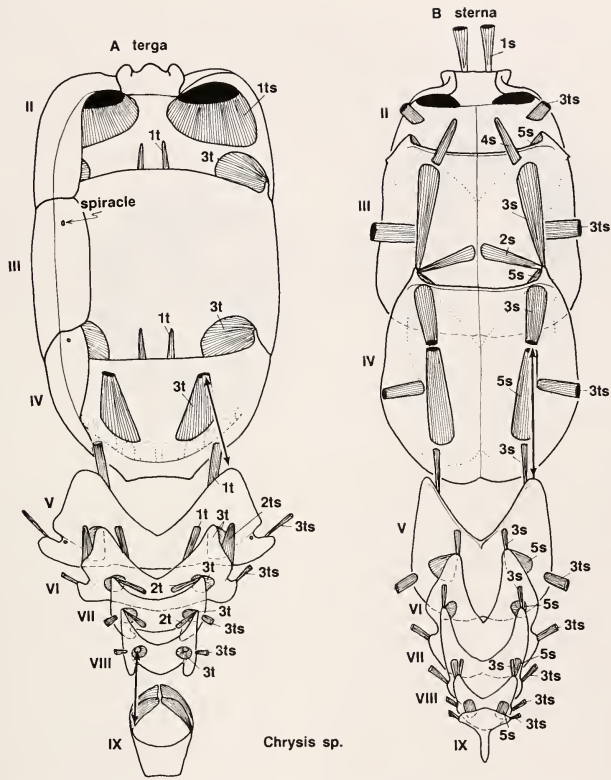


Fig. 4. *Chrysis* sp., male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

the anterior margin of the pit row (Fig. 4A), a row of ovoid depressions near the apical margin of the tergum. Segments V-VIII are differently shaped than the external segments, having strong anterolateral lobes on both the terga and sterna.

DISCUSSION

The internalization of abdominal segments allowed the chrysidids to develop a highly mobile and independently muscled ovipositor or genital tube. Several concurrent modifications are involved. The internalized segments retained their intersegmental musculature, with the associated

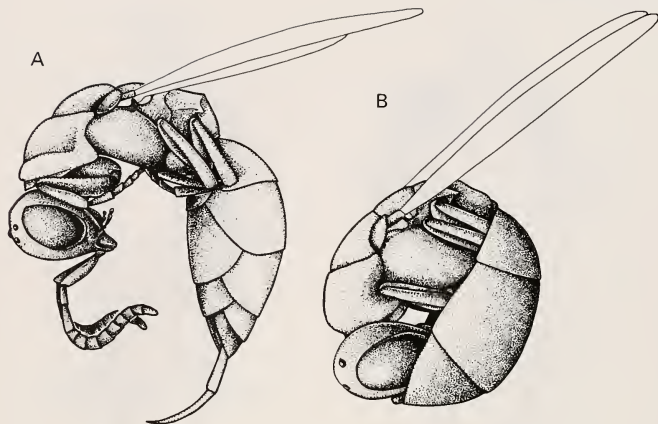


Fig. 5. Defensive posture of *Cleptes alienus* (A) and *Hedychrum* sp. (B).

enlargement of the tergal, sternal and tergosternal muscles, particularly 3t, 4s, 5s and 3ts. The intersegmental muscles, 3t, 5s and 4s, between the apical external segment and basal internal segment, serve as basal protractors and retractors of the tube. These are shifted in position and enlarged as shown in Fig. 4, where the origin of the major tergal protractor muscle, 3t, on tergum IV is situated submedially near the posterior margin of the tergum, and the muscle itself is elongate anteriorly. Contraction of this muscle pulls the anterior margin of tergum V nearly even with the posterior margin of IV. Relaxation of this muscle and contraction of 1t pulls the anterior apodemes of tergum V anteriorly, and nearly even with the anterior margin of IV. Muscle 5s on the sternum functions similarly. Therefore, exertion of the abdominal tube is primarily accomplished by contraction of 3t and 5s. The tube is telescoped within the abdomen at rest by contraction of 3s, 4s, 1t and 2t. In addition, retention of the intersegmental muscles on the tube segments enabled it to be flexible and mobile. The external segments have retained remnants of intersegmental muscles but these muscles are considerably reduced or lost in the case of those that function as tergal retractors (1t) and pronators (5s), or greatly enlarged as in the muscle that holds the

anterior tergal apodeme of a posterior segment to the side of the anterior tergum (3t), resulting in an almost complete loss of flexibility in the external segments in the Chrysidinae. Muscle 3t has a dual function in the Amiseginae and Chrysidinae. On the external segments 3t is very short and actually serves to limit movement between these segments. This muscle serves as one of the primary protractors of the internal segments and between these and the apical external segment.

Retracting the apical abdominal segments within the abdomen necessitated a change in the position of the muscle attachments between the apical external and basal internal segments. In chrysidids this muscle attachment has shifted from the base of the apical external segment to a submedial placement. Retraction is accomplished by contraction of 3s, 4s, 1t and 2t. In other aculeates these muscles (3s, 4s, 1t and 2t) serve to hold the abdominal segments tightly together and enable lateral, dorsal or ventral pronation, or allow limited posterior extension or elongation (3t and 5s).

The degree of modification of the intersegmental musculature varies from subfamily to subfamily, with the least occurring in the Cleptinae, and the greatest in Chrysidinae. The result is that in the Chrysidinae, where the largest number of seg-

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Mole Cricket Hunters of the Genus *Larra* in the New World (Hymenoptera: Sphecidae, Larrinae)

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Abstract.— Species of *Larra* in the New World are described, illustrated, their distributions summarized on maps, and a key for their identification provided. The known biologies are summarized and past efforts to introduce exotic species to the U.S. and Puerto Rico to control mole crickets are described. Eight species are recognized including one new one, *stangei*, from Bolivia and Argentina, and they are divided among three species groups. The females of two species, *bicolor* Fabricius and *praedatrix* Strand are inseparable. The following new synonymy is proposed: *Larrada gastrica* Taschenberg, 1870, *Larra guiana* Cameron, 1912, and *Larra scapteriscica* Williams, 1928 = *Larra bicolor* Fabricius 1804; *Larra paraguayana* Strand, 1910, *Notogonia gastrifera* Strand, 1910, and *Larra pacifica* Williams, 1928 = *Larra praedatrix* (Strand), 1910; *Larra braunsii* Kohl, 1898, *Larra transandina* Williams, 1928 = *Larra godmani* Cameron, 1889 (*godmani* is the first available name for the preoccupied species *Larrada aethiops* Smith, 1873). Species groups are used to arrange the species on a world basis, and the Old World subgenus *Cratolarra* Cameron is reduced to a synonym of *Larra*. Some characters that are important from a phylogenetic standpoint are analyzed for *Larra* and the other genera in the subtribe Larrina. A cladogram showing relationships of these taxa is provided. *Larra* is demonstrated to be derived from ground nesting ancestors.

The genus *Larra* has become important in recent years because of the need to find natural enemies of three neotropical mole crickets introduced to the southeastern United States. Mole crickets cause millions of dollars of damage yearly to turf and crops, and they cannot be controlled economically with chemicals. Thus, natural enemies offer the best hope for control. Wasps of the genus *Larra* are exclusive predators of mole crickets, but the New World species have not been identifiable with any degree of certainty due to the lack of a modern revision. Furthermore, choosing the right species of *Larra* for liberation in the U.S. depends on knowledge of their distribution in the Neotropical Region and their host preferences. This revision has resolved identification of the species (although there are still problems that need further study) and mapped their geographic ranges. Determination of host preferences is beyond the scope of my study, but now that the species of *Larra* are identifiable, other scientists can examine predator/host relationships more accurately.

When this study was initiated the New World fauna was represented by 16 species of *Larra* (Bohart and Menke, 1976), all but one of which were Neotropical. After examining the types of most of these, as well as descriptions of a few taxa whose types are missing, one species, *parvula* Schrottky (1903), has been transferred to the genus *Liris* (New

Combination), and two others listed by Bohart and Menke in the genus *Liris*, *gastrifera* Strand (1910) and *praedatrix* Strand (1910), have been transferred to *Larra* (New Combination). Considerable new synonymy has resulted in reducing the number of New World species of *Larra* to eight, one of which is new to science. These species have been segregated into three species groups.

Problems of species discrimination remain. For example, the two most abundant species in the New World, *bicolor* Fabricius and *praedatrix* (Strand), are separable only in the male sex, and the latter species has considerable genitalic variation. This variation may mean that there are more species than I have recognized, but resolution of this will probably require rearing experiments, or more sophisticated techniques such as cuticular hydrocarbon analysis, not to mention more intensive collecting. In summary, *Larra* is a frustratingly difficult genus, and it is sure to tax the ability of the next person who studies it.

INSTITUTIONS LENDING MATERIAL

I have examined over 4200 specimens during this study. They were borrowed from the following collections. Parentheses enclose the name of the contact person and capitalized symbols used to identify sources of material cited in the text.

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- Zoologisk Museum, Copenhagen, Denmark (Ole Lomholdt) (COPENHAGEN)

BIOLOGY

Bohart and Menke (1976) summarized the literature on *Larra*. Since then, a number of papers have been published on *Larra bicolor* by workers associated with the introduced mole cricket problem in Florida, principally James L. Castner. Much of this subsequent literature was summarized by Castner (1988), and the account that follows, unless stated otherwise, is taken from that paper.

Larra bicolor Fabricius

Foraging.—Floral visitation occurs from about 8:30AM to 3:30PM with males predominating in the morning. In Puerto Rico *L. bicolor* most commonly visits flowers of *Spermacoce verticillata* L. (Rubiaceae), but *Croton glandulosus* L. and *Euphorbia heterophylla* L. (Euphorbiaceae), both of which have extrafloral nectaries, are also favorites.

In Bolivia *L. bicolor* visits *Cissus* sp. (Vitaceae) almost exclusively if it is flowering, but *Spermacoce verticillata*, *Euphorbia* sp., and occasionally *Mikania micrantha* (Compositae) are attractive to the wasp (Bennett and Pruett, 1991).

Mating.—Chemoreception of a female pheromone is apparently used by the male to locate the opposite sex when several meters away, but once near the potential mate, vision is used to home in on her. Females are approached from behind, the male attempting to mate by either running up on her, or flying directly on to her. Castner (1988) stated that females foraging on flowers are never approached, and that only females on the ground were mated, but Bennett and Pruett (1991) commonly observed males searching for females in foliage.

Actual mating has rarely been observed. According to Bennett and Pruett (1991), once a male has landed on a female, she raises her abdomen if

she is receptive, and the male engages her for less than five seconds ("... it is almost a non-event"). Afterwards both individuals groom the tip of the abdomen with their hindtarsi.

Prey searching.— This activity occurs from about an hour after sunrise to 3:45 PM. Prey searching occurs on cloudy, overcast days as well as sunny ones, but not apparently on rainy days. Typically the female walks over the ground until a mole cricket surface gallery is encountered, whereupon she excavates down into it and enters the tunnel. Just what happens between wasp and mole cricket in the burrow is unknown, but the orthopteran typically evades the wasp by surfacing. According to Castner, surfacing mole crickets escape capture by the wasp about 50% of the time. Wasps return to the surface often apparently to determine if the host has surfaced. Small nymphs are attacked as well as large adults.

Paralysis of prey.— The female captures the surfaced mole cricket. She then stings the host repeatedly in a fixed pattern: to the base of the fore and midlegs, and to the base of the palpi. Paralysis generally lasts for 3 to 4 minutes. If the cricket revives before oviposition is complete, more stings are administered. Once the mole cricket is paralyzed, the wasp often turns it on its back and chews at the base of one of the forelegs, appearing to feed on exuding body fluid.

Oviposition.— Prior to oviposition the wasp usually rubs the tip of her abdomen over the ventral area of the mole cricket, possibly to determine if a wasp egg or larva is already present. If an egg is detected, the wasp initiates a searching/biting behavior that may take several minutes before the egg is removed (Castner, 1986). In experiments females would even remove their own eggs from mole crickets. The egg is attached in the soft, membranous tissue between the first and second pair of legs of the host, lateral to the midventral line. After deposition of the egg, the wasp then either flies away or remains with the host until it revives and re-enters the ground. Some wasps have been observed to chase away foraging ants.

Larval development.— Under laboratory conditions eggs hatch in 6-7 days. The first instar larva feeds on hemolymph at the site of egg attachment and after 8-9 days has progressed through four instars, growing slowly all the while. One to three days later the fifth and final instar has killed the host, consumed the soft, inner tissues and grown suddenly to a length of 14-26 mm. In about a day the mature larva spins a cocoon in the mole

cricket's gallery. An adult wasp emerges 6-8 weeks later.

Host suitability.— *Larra bicolor* is not necessarily host specific, at least under laboratory conditions in Florida, where the wasp was able to develop on five neotropical species of *Scapteriscus* mole crickets (*abbreviatus* Scudder, *borelli* Giglio-Tos (*acletus* Rehn and Hebard is a synonym, see Nickle 1992), *vicinus* Scudder, *didactylus* (Latreille), and *imitatus* Nickle and Castner), the first three of which are established in the state. However, survival on *S. didactylus*, an exotic species so far not known in the U.S., was significantly less than in the other four, suggesting possession of some type of anti-parasite mechanism by the host. Similar results were obtained in laboratory tests in Bolivia with four species of *Scapteriscus* (Pruett and Bennett, 1991), but *bicolor* preferred *S. vicinus* Scudder. In laboratory studies, *L. bicolor* reluctantly accepted the native Floridian mole cricket *Neocurtilla hexadactyla* (Perty), whose range also includes much of South America (Castner, 1988, Pruett and Bennett, 1991). But this mole cricket has a defense mechanism: it secretes a viscous anal fluid that entangles the attacking wasp, thus permitting the prospective host to escape. In Bolivian laboratory trials, Pruett and Bennett demonstrated that of 328 *bicolor* eggs successfully laid on *N. hexadactyla*, only 5 developed to the pupal stage, and many died in the first instar. Apparently this mole cricket has more than one mechanism for dealing with its attackers.

Larra analis Fabricius

Smith (1935) extensively studied the only native North American *Larra*, and his account shows that *analis* has basically the same behavior as *bicolor*. This wasp attacks *Neocurtilla hexadactyla*, the native North American mole cricket. Smith observed that wasps sometimes were entangled by the same sticky substance that this mole cricket used to thwart attacks by *bicolor*. The only difference in the behavior of *analis* is that the egg is attached behind the hindleg. Development from egg to cocoon ranged from 12 days in mid summer to about 30 days in the fall.

Egg placement behind the hindleg was noted by Williams (1928, p. 42) in an unidentified species from Tena, Ecuador. The only species from Tena represented by females in Williams' material (BISHOP & USNM) are *godmani* (Cameron) and *altamazonica* Williams, both of which belong in the *analis* species group. Egg placement behind the

hindleg of the host may thus be a feature of the *analis* group.

Larra godmani Cameron

Two females that I have studied, one from Chapare, Bolivia, and one from Cauqueta, Colombia, have prey pinned beneath them. Both are immatures of a species of *Neocurtilla* (det. D. Nickle). Bennett et al. (1990) state that in Bolivia this *Larra* (as *braunsii*) attacks medium to large nymphs of *Scapteriscus vicinus* and small nymphs of *S. borellii* (as *acletus*).

INTRODUCTIONS TO CONTROL MOLE CRICKETS

Hawaii.—Introductions of exotic mole crickets to Hawaii, Puerto Rico, and the southeastern US prompted a search for control agents. F. X. Williams pioneered the research on *Larra* as a control agent. He explored the Philippines and Australia in an effort to find natural predators for *Gryllotalpa africana* (Palisot de Beauvois), established on the islands of Oahu and Kauai. In 1921 and 1925 he sent live material of *Larra luzonensis* Rohwer collected in the Philippines to Hawaii, and it was liberated at various sites on Oahu where it became established (Williams, 1928). He also liberated another Philippine species, *L. amplipennis* (Smith) (as *L. sanguinea*), in 1922 but it failed to become established.

Williams then turned to South America in his search for an effective species of *Larra*. He sent material of *Larra bicolor* (as *americana* and *scapteriscica*) taken in Belém, Brasil, to Hawaii in 1924, but the introduction failed.

Puerto Rico.—George Wolcott (1941) sought predators of mole crickets at Belém, Brasil, where F. X. Williams (1928) found *Larra* to be common. Between 1936 and 1940 Wolcott and his associates liberated a number of collections of *L. bicolor* in Puerto Rico, and the species became established there. Of particular interest was the discovery that survival of live wasps in transport was greatly enhanced when live but paralyzed mole crickets accompanied them. This technique resulted in the accidental introduction to Puerto Rico of another species of mole cricket, however (Nickle & Castner, 1984).

Florida.—Three exotic species of mole crickets of the genus *Scapteriscus* were introduced into the southeastern U.S. around the turn of century

(*abbreviatus*, *borellii*, and *vicinus*). Now well established, they cause considerable damage to turf and pasture grasses, especially *vicinus*. It is estimated that in Florida alone these herbivores cost in excess of \$44 million annually when damage and control measures are tallied (Hudson, et al., 1988).

In the late 1970's scientists at the University of Florida began investigating potential predators and parasites, and by 1981 had released *Larra bicolor* from Puerto Rico at three sites in Florida: Gainesville, Tampa, and Fort Lauderdale (Hudson, et al., 1988). Subsequent releases were made at Bradenton and Lakeland in 1982-83. The wasp became established only at Fort Lauderdale, presumably either because the other sites were too cold for winter survival of an essentially tropical wasp, or because too few wasps were released or they were too old. Currently searches for suitable *Larra* for introduction to northern Florida have been centered in Bolivia. Bolivian material of *L. bicolor* and *L. godmani* (as *braunsii*) was liberated at several sites in Alachua Co. in 1988-89 (Bennett et al., 1990). The success of these releases has not been evaluated.

Among material of *L. bicolor* assembled for this revision is a single female collected at Watson's Hammock, Big Pine Key in Monroe Co., Florida, in 1986 (ALBERTA). This site is far from Fort Lauderdale, and it may represent a hitherto undetected natural population of *L. bicolor*, or a chance introduction. As pointed out in the systematic treatment of this species, it is possible that this Big Pine Key female is actually the species *L. praedatrix*.

RECOMMENDATIONS FOR INTRODUCING LARRA TO FLORIDA

The three introduced mole crickets in the southeastern U.S. originated in southern South America, primarily the region around Buenos Aires, Argentina (Nickle and Castner, 1984). Thus it would seem most rewarding to collect *Larra* from that region for introduction to the U.S. Also, the climate there is temperate, rather than tropical, and the wasps would have a better chance of surviving in North America, especially if collected south of the 30th Parallel. Four species of *Larra* occur commonly in the area around Buenos Aires: *burneiserii*, *bicolor*, *praedatrix*, and *princeps* (the last three belong in the *bicolor* group). Any of these species may be good candidates for introduction to Florida, and in fact, *L. bicolor* from Puerto Rico has been successfully

introduced there. It survived only in southern Florida, however, and introductions of *L. bicolor* from a more temperate region such as northern Argentina would seem more logical. Prey specificity for species of *Larra* is poorly understood at present, and the mole crickets attacked by *burmeisterii*, *praedatrix*, and *princeps* are unknown. *Larra princeps* in particular would seem worthy of study, because it has the southernmost range in South America of any species in the genus (nearly to the 40th Parallel) and thus may be expected to survive in the cooler parts of the southeastern U.S.

Genus LARRA Fabricius

Larra Fabricius, 1793:220. Type species: *Larra ichneumoniformis* Fabricius, 1793 (= *Sphex anathema* Rossi, 1790), designated by Latreille, 1810.

Larrana Rafinesque-Schmaltz, 1815:124. Emendation of *Larra* Fabricius.

Larra Drapiez, 1819:54. Lapsus or emendation of *Larra* Fabricius. *Monomatium* Shuckard, 1840:181 (no species). Type species: *Larraxena princeps* F. Smith, 1851, designated by Pate, 1935 (first included species).

Lyrops Dahlbom, 1843:132. Type species: *Tachytes paganus* Dahlbom, 1843, monotypic. Not *Lyrops* Illiger, 1807.

Larraxena F. Smith, 1851:30. Type species: *Larraxena princeps* F. Smith, 1851, monotypic.

Larrada F. Smith, 1856:273. Type species: *Larrada anathema* (Rossi), 1790, original designation.

Cratolarra Cameron, 1900:34. Type species: *Cratolarra femorata* Cameron, 1900, monotypic. NEW SYNONYM.

The extensive generic description in Bohart and Menke (1976) is generally quite thorough, but one structure was insufficiently described, and two others not mentioned. The female scape was described as conspicuously shining in contrast to the flagellum in many species, and while that is true, it is important to add that it is also largely asetose and impunctate in those species (Fig. 8). The pronotum in *Larra* usually has a transversely elongate sulciform depression anteromedially, although in some species there are two oval pits in the same position that may be narrowly joined. Finally, in many species of *Larra*, the inner surface of the forebasitarsus has an asetose linear polished zone (Fig. 28). It occurs in both sexes but is best developed in the female. In a few species the basitarsus is setose throughout (Fig. 26) as in *Liris*, or has a small, rather poorly defined asetose area (Fig. 27).

The difficulty in separating *Larra* from the genus *Liris* was well documented by Bohart and Menke (1976:235, 240). The polished, asetose zone present

on the inner surface of the forebasitarsus of many species of *Larra* is an additional difference from *Liris*, but unfortunately it is not universal. The apparent differences in the biology of these taxa argue for maintaining *Larra* as a separate genus, but the problem of finding clear morphological differences remains.

Subgenera and species groups.—Bohart and Menke (1976) recognized two subgenera that were differentiated by the presence (*Larra*) or absence (*Cratolarra*) of spine rows on the foretibia. After examining 25 of the 60 species in the genus I have reached the conclusion that *Cratolarra* is only one of several recognizable groups within *Larra*, and certainly no more distinct than the others. My phylogenetic analysis confirms this and therefore I am synonymizing *Cratolarra* (NEW SYNONYM). I am using species groups to segregate the taxa of *Larra*. The Old World *Cratolarra* becomes the *maura* group, its name based on the oldest species in the group. Tsuneki (1967) called it the *carbonaria* group. Other Old World groups recognized by me include the *amplipennis* and *anathema* groups. The New World species are divided among the *bicolor*, *burmeisterii*, and *analis* groups. They are characterized later in the paper.

The *amplipennis* group includes species with a setose forebasitarsus, a setose female pedicel, a largely asetose polished frons in the female (an apomorphy), a flat non-beveled labrum, spine rows on the female foretibia (an apomorphy), and placoids on most flagellomeres of the male. In addition the female lacks an ocular sinus. Species examined from this group include *amplipennis* (Smith) and *betsilea* Saussure.

The *anathema* group shares most of the characters of the *amplipennis* group. But the female pedicel is largely asetose and polished dorsally, and the forebasitarsus has a poorly defined asetose zone on its inner surface; both are apomorphies. I have examined *anathema* (Rossi) and *melanocnemis* Turner. The last species is only provisionally assigned to the group.

The *maura* group lacks spine rows on the female foretibia, a character that sets it apart from all other species of *Larra*. I regard this state as plesiomorphic in *Larra* but my phylogenetic analysis suggests that in the *maura* group the absence of spines is a reversal (see Cladogram). The female pedicel is completely asetose and polished, the female frons is asetose and polished, the female upper interocular distance is less than half the lower interocular distance, and

the female vertex has a deep sinus around the inner eye margin - all apomorphies. In addition, the labrum is flat, not beveled apically, and the male has placoids on most flagellomeres; both are plesiomorphic features. Species of this group that I have examined are: *carbonaria* (Smith), *femorata* (Saussure), *fenchihuensis* Tsuneki, *heydenii* Saussure, *huzonensis* Rohwer, *maura* (Fabricius), *outeniqua* Arnold, *polita* (Smith), *saussurei* Kohl, and *variipes* Saussure.

Species characters.— New World *Larra* have exasperatingly few characters. Some of those used by Williams (1928) such as thoracic punctation, presence or absence of a median carina on the propodeal dorsum, body and wing color, and details of the female vertex are unreliable. Other features used by Williams are really group characters: female pedicel asetose, polished, and female vertex with ocular sinus. He was unaware of the value of placoid distribution on the male antenna as a species character for members of the *analis* group. On the other hand Williams used male genitalia and I have found them to be very important in the *bicolor* and *burmeisterii* groups. The genitalia of species in the *analis* group seem identical. The genitalic variability observed in some *bicolor* group species is perplexing and needs further study. The shape of the female pygidial plate is diagnostic for some species.

I have compared the upper interocular distance (UID) to the lower interocular distance (LID), but there is considerable variability in some species (20+ specimens measured on average) and overlap between some species. I made my measurements with an ocular micrometer at a magnification of 50X. Figures 1-4 illustrate how these measurements are made, and proper head orientation. Williams (1928) used the lengths of the pedicel and flagellomeres I-II and compared them to the upper interocular distance, but they are not any more reliable or meaningful than UID/LID comparisons.

Character analysis.— In order to assess the relationships of the species involved in this study, and the position of *Larra* itself within the Larrinae, I have attempted to polarize a number of characters. My outgroup consisted of the other genera of the subtribe Larrina: *Liris*, *Dalara*, *Paraliris* and *Dicranorhina*, although I have sometimes referred to taxa in the subtribe *Tachytina*. Bohart and Menke (1976) regarded *Larra* as the most primitive member of the subtribe Larrina, and *Paraliris* and *Dicranorhina* as the most derived. That may be true, but I think

that I can now demonstrate that some character states regarded by Bohart and Menke as plesiomorphic in *Larra* are really apomorphic.

In my analysis 0 = the plesiomorphic state, and 1 and 2 = apomorphic states (and do not necessarily represent transformation series). Characters 14-17 were not used in the phylogenetic analysis because they do not appear to be particularly informative, but they are included here because they may merit further study.

1. *Labrum*: 0 = flat, not broadly beveled or sloping down at apex, not emarginate; 1 = surface sloping down at apex, or broadly beveled there, free margin arcuate, obtusely angular, or lobate.

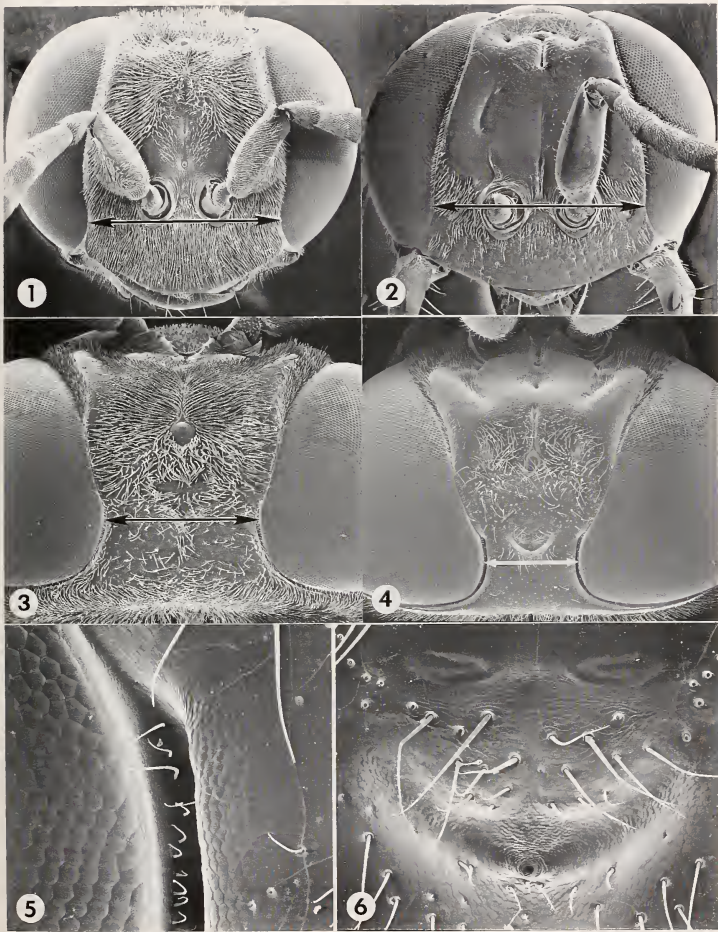
The plesiomorphic state is apparently universal in the outgroup, in all Old World *Larra*, and the monotypic *burmeisterii* group (Fig. 15) in the New World. The apomorphic state is present (Figs. 16-18, 55) in the *bicolor* and *analis* groups of *Larra*, both restricted to the New World. In the single species of *Paraliris* available, the labrum is flat, but the free edge is quite thick, and in *Dicranorhina* and some *Liris* the labrum has an apical emargination. These represent other apomorphic states. In the *Larra bicolor* and *analis* groups it is my assumption that the labrum has become elaborated to aid excavating.

2. *Female antennal pedicel*: 0 = surface densely setose, similar in appearance to flagellomeres; 1 = dorsum sparsely setose, or asetose, remainder densely setose; 2 = surface largely asetose, polished, contrasting with setose flagellum.

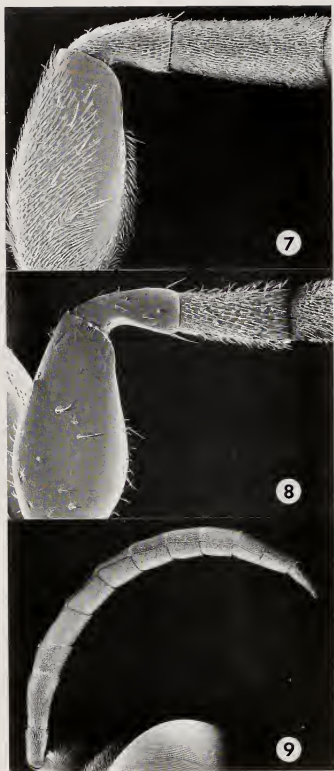
The plesiomorphic state appears to be universal in the outgroup, as well as in the New World *bicolor* group (Fig. 7) and the Old World *amplipennis* group of *Larra*. The apomorphic state is universal in the Old World *maura* group, as well as in the *burmeisterii* and *analis* groups (Fig. 8). The pedicel of two Old World *Larra* is intermediate. In the Australian species *L. melanocnemis* Turner, the pedicel is more or less asetose dorsally but setose elsewhere. In the Palearctic species *L. anathema* (Rossi) it is sparsely setose dorsally, and densely setose elsewhere.

3. *Placoids of male flagellum*: 0 = present on all but the first one or two flagellomeres; 1 = present on only a few flagellomeres; 2 = absent.

In the majority of the species of *Liris* examined, placoids are present on flagellomeres II-XI. Exceptions occur in the subgenus *Motes*, where some species have only a single placoid, and others have a full complement. In *Larra* all species have the plesiomorphic condition (Fig. 9) except members of the *analis* group (Figs. 13, 59-62). The



Figs. 1-6. Head details of *Larra*. 1-2, Face showing how to measure lower interocular distance and orientation when doing so. 1, Male of *bicolor*. 2, Female of *altamazonica*. 3-4, Top of female head showing how to measure upper interocular distance and proper orientation. 3, *bicolor*. 4, *godmani*. 5-6, Details of female vertex of *godmani*. 5, Ocular sinus along orbit of left eye. 6, Depression behind hindocelli showing pore at bottom.



Figs. 7-9. Antennal features of *Larra*. 7-8. Left female scape, pedicel, and flagellomere I. 7, *bicolor*. 8, *altamazonica*. 9. Right male antenna of *bicolor*.

intermediate apomorphic state occurs in the latter group and *Dalara*. The most apomorphic state occurs only in *Paraliris* and *Dicranorhina*. Bohart and Menke (1976) regarded the absence of placoids as plesiomorphic in the Larrinae, but in the subtribe Larrina I think the most logical assumption is that presence of placoids on most flagellomeres is the

plesiomorphic condition, and that loss of placoids is the apomorphic condition - a reversal. This is supported by the fact that species and genera in which reduction or complete loss of placoids has occurred are recognizable as derived by other character states. For example, the *analisis* group, which has only 2 to 4 placoids, has an apomorphic labrum, female pedicel, female orbital sinus, and female foretibial carina.

4. *Orbital sinus*: 0 = absent; 1, present, narrow, 2, present, broad.

A deep sinus around the upper orbit of the eye, especially in the female, is apparently absent in the outgroup as well as many species of *Larra*. A narrow sinus is usually present in the female of the monotypic *burmeisterii* group (Fig. 49). All members of the *analisis* group and the Old World *maura* group have a broad, deep sinus (Fig. 4). It is best developed in the female but is present in males as well. The function of this depression (Fig. 5) is unknown.

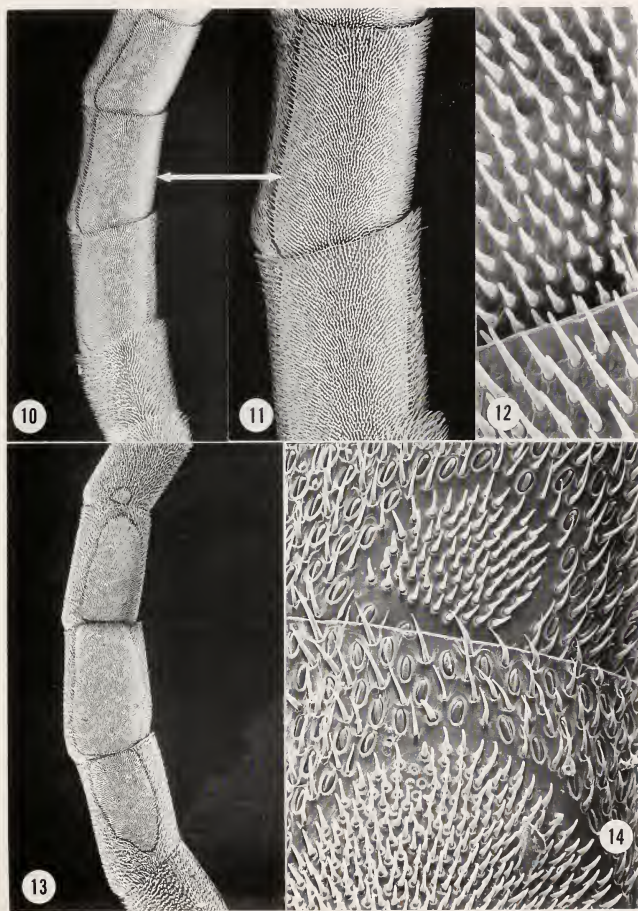
5. *Female frons*: 0 = dull, setose; 1 = polished, largely setose; 2 = polished, largely asetose.

In the outgroup the frons beneath the transverse swelling is usually covered fairly densely with setation that obscures the integument which is usually dull. In nearly all female *Larra* the frons is asetose or nearly so (Fig. 2), the integument easily visible and polished. I regard this as an apomorphy. In the *Larra bicolor* group the frons is setose at least laterally (Figs. 39-40) but the integument is shiny - this represents an intermediate condition.

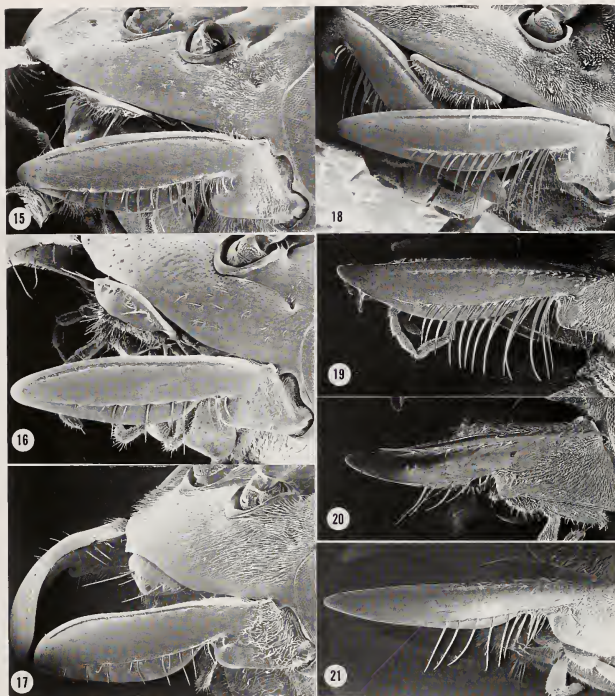
6. *Female mandible*: 0 = cutting edge with one or two subbasal teeth; mandible strongly arched from base to apex, outer surface somewhat angled in cross-section, narrow distad of posterobasal notch and attenuate to apex (pick-like); 1 = cutting edge without teeth; outer surface evenly curved in cross-section, broad beyond posterobasal notch almost to apex (scoop-like).

Bohart and Menke (1976, p. 224, 243) considered absence of teeth on the cutting edge to be plesiomorphic in *Larra*, but I believe that this state is apomorphic since teeth are nearly universally present in the outgroup, one exception being the subgenus *Motes* of *Liris*. Teeth are also absent in the specialized genus *Parapiagetia*, and some specialized species of the genera *Gastrosericus* and *Tachysphex* (all subtribe *Tachytina*). I hypothesize that teeth have some function in prey transport, and because female *Larra* do not carry their prey, they have lost the teeth.

The overall form of the mandible is most often pick-like in the outgroup (Figs. 20-21), but in *Larra*



Figs. 10-14. Male flagellar details of *Larva* showing placoids. 10-12, *L. bicolor*. 10, Flagellomeres II-V with placoids on III-V. 11, Flagellomeres IV-V. 12, Setal structure of placoids on flagellomeres IV-V. 13-14, *L. analis*. 13, Flagellomeres II-VI showing placoids on III-VI. 14, Setal structure of placoids on flagellomeres V-VI.



Figs. 15-21. Details of female mouthparts in *Larra* and *Liris*. 15-18, Clypeus, labrum and left mandible in *Larra*. 15, *burmeisterii*. 16, *altamazonica*. 17, *godmani*. 18, *bicolor*. 19-21, Left mandible. 19, *Larra stangei*. 20, *Liris niger*. 21, *Liris bembesianus*.

it is often a broad, scoop-like structure (Figs. 15-17) that I hypothesize has evolved in response to their habit of simply digging down into mole cricket burrows that generally are in damp soil. Presumably the scoop form offers a more efficient digging implement than a spike-like mandible. Similar scoop-like mandibles occur occasionally in *Liris* and elsewhere in the subfamily Larrinae. Widening of the area beneath the condylar groove (Michener and Fraser 1978) contributes to the formation of the scoop in some *Larra* (Figs. 15-17).

7. *Mandibular notch*: 0 = present, located near middle of mandible; 1 = present, located close to

mandible base; 2 = reduced to small V or absent.

The function of the mandibular notch is unknown. I (Menke, 1988) came to the conclusion that the absence of a mandibular notch is plesiomorphic in the subfamily. This is clearly the generalized condition in the entire family Sphecidae. However, within the Larrinae notchless mandibles are common only in a few taxa; some examples are: *Solierella* (Miscophini), most Crabronini, *Oxybelus* (Oxybelini), and *Pison* and *Trypoxylon* (Trypoxylini). Complicating the hypothesis are the apparent reversals scattered through the Larrinae. The notch seems to have been

reduced or lost in various specialized taxa; examples are found in *Liris*, *Gastrosericus*, *Holotachysphex*, and *Tachytes*. Clearly the notch in Larrinae needs further investigation. In most members of the outgroup, as well as most genera of Larrinae, the notch is located near the middle of the mandible (Fig. 20), or slightly more basal. In *Larra*, however, it is clearly subbasal (Figs. 15-19), due in part to lengthening of the outer part of the mandible. I hypothesize that this has enhanced development of the mandible's scoop-like form. Some *Liris* with well developed tarsal rakes have elongate mandibles and the notch in these is subbasal (Fig. 21). The mandibular notch is just a small obtuse V in *Liris* subgenus *Liris*, and in one species of *Paraliris*, or is absent just as in *Dalara* and most *Paraliris*. The mandible of the latter two genera is otherwise specialized (shape, and extra teeth) which suggests to me that the absence of a notch is a loss feature (apomorphic) in Larrina. The reduction in *Liris* (*Liris*) is interpreted similarly.

8. *Setae of condylar groove of female mandible*: 0 = setae fine, not particularly stiff, not clearly rake-like (Fig. 20); 1 = setae numerous, thickened, stiff, forming a rake (Figs. 18-19, 40); 2 = setae weak, scattered, rake poorly developed (Figs. 15-17).

In most *Larra* the setae in the condylar groove (Michener and Fraser 1978) are numerous, thickened and stiff, forming a rake. Presumably it aids in digging. In the New World *analisis* group the rake setae are widely spaced and rather short (Figs. 16-17). Presumably this condition is a reversal since some species in this group have a well developed scoop-like mandible. Generally in the outgroup the setae are finer and appear less effective as a rake. There are exceptions in *Liris* (Fig. 21), some species of which excavate very deep nests.

9. *Apex of female mandible*: 0 = simple; 1 = bidentate.

A simple apex is the ground plan condition in the subtribe Larrina, and indeed in the family Sphecidae. However, the apex is bidentate in the female of *Dalara* and in both sexes of *Paraliris* (exceptional males of one species lose the condition - see van der Vecht, 1981), an obvious apomorphy. At least one species of *Liris*, *tenebrosus* (Smith) from South America, also has a bidentate female mandible, but this is not the ground plan in this very large genus.

10. *Female foretibial spine rows*: 0 = absent; 1 = one row present; 2 = two (Fig. 23) or three present (Fig. 22).

In the outgroup the foretibia does not have a

row of stout setae except in *Liris* s.s., a few species of which, principally the non-insular taxa, have a single row. On the basis of other features, the subgenus *Liris* is a highly evolved lineage, and the foretibial setal row is apparently an apomorphic trait. The African species, *Liris* (*Leptolarra*) *croesus* (Smith), has two rows of setae, one of which consists of two or three setae. Presumably the spine rows aid in excavating; all *Liris* with them have well developed foretarsal rakes.

In *Larra* the Old World *maura* group lacks spine rows, but in the rest of the genus there are two or three rows. Commonly specimens of the *bicolor*, *burmeisterii* and *analisis* groups actually have three rows, the innermost one closely paralleling the next and consisting of two to four somewhat finer spines (Fig. 22). Because the rare occurrence of one or two spine rows in *Liris* is obviously not the ground plan condition in that very large genus, it has been omitted from the phylogenetic analysis. Thus in the analysis, condition 1 represents the presence of 2 or 3 spine rows as in *Larra*.

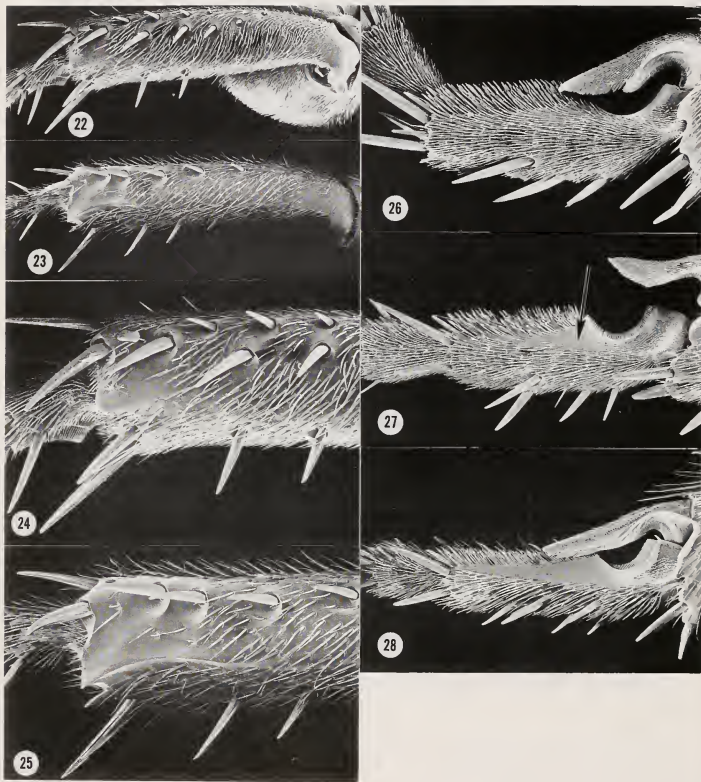
11. *Female foretibial carina*: 0 = absent (Fig. 24); 1 = present (Fig. 25).

In the outgroup and most *Larra* the outer apex of the tibia lacks a carina. In the *analisis* and *burmeisterii* groups however, there is a carina adjacent to the smooth, asetose zone at the apex. I regard this as an apomorphy.

12. *Female forebasitarsal asetose zone*: 0 = absent (Fig. 26), 1 = present (Fig. 27); 2 = present, extending to apex of segment (Fig. 28).

In the outgroup and in the *Larra* *amplipennis* group the basitarsus is setose within. Also one species in the *Larra* *bicolor* group, *stangei*, has an entirely setose forebasitarsus (Fig. 26). In the remaining groups of *Larra* the inner surface of the basitarsus distad of the basal cleaning notch has an impunctate asetose zone of variable length. This zone is a polished strip that attains the apex of the segment in the *burmeisterii*, *analisis* and *maura* groups (Fig. 28). I regard this as the most derived state. An intermediate state is found in the *bicolor* and *anathema* groups (Fig. 27), although one species in the *bicolor* group, *stangei*, exhibits the plesiomorphic condition.

13. *Biology*: 0 = captures and paralyzes prey, places prey in previously constructed nest cell and then lays an egg; 1 = temporarily paralyzes host, deposits egg, then flies away, host revives and re-enters burrow, host's burrow functioning as chamber for wasps' pupa.



Figs. 22-28. Details of left front tibia and basitarsus of female *Larra*. 22-23, Outer surface of tibia. 22, *bicolor*. 23, *godmani*. 24-25, Outer surface of tibial apex. 24, *bicolor*. 25, *godmani*, showing carina. 26-28, Inner surface of female basitarsus. 26, *stangei*. 27, *bicolor*, arrow points to asetose zone. 28, *godmani*.

Bohart and Menke (1976, p. 2, 227, 237) considered the parasitoid-like biology of *Larra* to be among the most primitive in the Sphecidae. I think however, that a different hypothesis can be made, one that results in *Larra*'s biology being considered apomorphic in *Larrina*. I propose that *Larra* has

abandoned the nest preparation habit of its ancestors, and adopted the burrow of its mole cricket host as its nest. Female morphology supports this hypothesis. A pygidial plate is used by larrine wasps as a tamping device during nest closure. *Larra* has a pygidial plate, but has no apparent use

for it because these wasps have no nest to seal. I think the plate in *Larra* is a relic from its nest building ancestors. The only excavating that *Larra* does is digging into the burrow of the mole cricket host. I hypothesize that the scoop-like mandible and mandibular rake setae common to most female *Larra* evolved to make them more efficient diggers. The spine rows on the foretibia of many *Larra* presumably have a similar explanation. Outgroup members, all of which, so far as known, transport prey after paralysis, have teeth on the cutting edge of the mandible (*Liris* subgenus *Motes* an exception) that presumably aid in grasping prey. *Larra*, which does not transport prey, has lost these teeth. The biology of the outgroup is still fragmentary or unknown except in *Liris*, and even here only a few of the nearly 300 species have been observed (Bohart and Menke, 1976, Kurczewski and Spofford, 1987). But this small data base suggests that the ground plan for the subtribe *Larrina* is for females to use pre-existing burrows or cavities for nest sites. Morphologically derived taxa like *Dicranorhina* excavate new burrows that may be maintained for several generations. Excavated burrows may be very deep as in *Liris* subgenus *Liris*.

The egg of *Larra*, at least in some Old World species, is much smaller in comparison to the size of the wasp (1.75 mm for egg, 16-19 mm for wasp) than in *Liris*, and is glued along most of its linear length to the host, presumably to prevent dislodgement by the mole cricket (Williams, 1928:38), rather than at one end as in other *Larrina*. If these two traits are apomorphies, they would support my thesis that the biology of *Larra* is specialized, rather than primitive. Egg size apparently is not always comparatively small, however, since Castner (1988) states that eggs of *Larra bicolor* are 4.0-4.5 mm long (female wasps range in size from 9.5-20 mm). Also it is not clear from published accounts that *Larra* eggs are never attached only by one end to the host.

The following characters were not used in the phylogenetic analysis.

14. *Vertex*: 0 = Upper interocular distance more than half as wide as lower interocular distance; 1 = UID less than half as wide as LID.

Both states occur in *Larra* as well as most of the outgroup. Narrowing of the UID is regarded by sphecoid workers as an apomorphy in the family. State 1 occurs occasionally in the *bicolor* and *burmeisterii* groups too. The apomorphic condition predominates in the *analis* group and the Old World

maura group, both of which have a well developed orbital sinus, another apomorphy. Because of overlap between the two states in nearly each species group of *Larra*, this character is not particularly informative. Nevertheless, trends are apparent in some groups.

The vertex has a central U or V-shaped depression just behind the hindocelli which contains a pore-like opening that may have a glandular function (Fig. 6).

15. *Pronotal pit (-s)*: 0 = transversely elongate; 1 = two transversely elongate pits present that are narrowly separated; 2 = two oval pits present.

I (Menke, 1988) demonstrated that the presence of some kind of pit or pits on the pronotal midline anteriorly was an apomorphy in Sphecidae. In the *Larrina* three basic conditions can be defined. The common one in the outgroup is a single, transversely elongate sulcus, but a pair of elongate pits occurs in *Dalara* and some *Liris*, particularly the subgenus *Liris*, although also in a few species of the subgenus *Leptolarra*. In some *Dicranorhina* there are two pits narrowly joined by a bridge. All Old World *Larra* that I have examined have a single, transversely elongate sulcus and so do most members of the New World *bicolor* group. The *analis* and *burmeisterii* groups have a pair of separate oval pits (narrowly joined in one species). Polarization here is obviously a difficult decision but I am hypothesizing that paired oval pits is the most derived state in *Larrina*.

16. *Submarginal cell of forewing*: 0 = four sided, 1 = three sided, the inner and outer veinlets joining forming a petiole that reaches the marginal cell (Fig. 45).

Petioloation of submarginal cells is widely regarded as a specialization in Sphecidae. All members of the outgroup have the plesiomorphic state, but at least two species of *Larra* display the apomorphic condition (*princeps* (Smith) and *dux* (Kohl)).

17. *Color of abdomen*: 0 = black, 1 = red and black, 2 = red.

A black abdomen (and body in general) is the common state in the outgroup. Some species of *Dicranorhina*, one of the more specialized genera in the subtribe *Larrina*, have red color on parts of the body. In the large genus *Liris*, red occurs in very few species and is usually confined to the legs, but *rubricatus* (Smith), *rubellus* (Smith) and several others, have a red abdomen. Thus black seems to be the ground plan state, and red a derived condition. A black abdomen is apparently universal in the

Table 1. Data matrix for species groups of *Larra* and other genera of subtribe Larrina.

Taxa	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dicranorhina</i>	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Paraliris</i>	0	0	2	0	0	0	2	0	1	0	0	0	0
<i>Dalara</i>	0	0	1	0	0	0	2	0	1	0	0	0	0
<i>Liris</i> (<i>Liris</i>)	0	0	0	0	0	0	2	0	0	0	0	0	0
<i>Liris</i> (<i>Motes</i>)	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Liris</i> (<i>Leptolarra</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Maura</i> group	0	2	0	2	2	1	1	1	0	0	0	2	1
<i>Amplipennis</i> group	0	0	0	0	2	1	1	1	0	1	0	0	1
<i>Anathema</i> group	0	1	0	0	2	1	1	1	0	1	0	1	1
<i>Analís</i> group	1	2	1	2	2	1	1	2	0	2	1	2	1
<i>Burmeisterii</i> group	0	2	0	1	2	1	1	1	0	2	1	2	1
<i>Bicolor</i> group	1	0	0	0	1	1	1	1	0	2	0	1	1

Larra maura group, although some species have red legs. A mixture of black and red occurs in the *amplipennis* and *anathema* groups but I have not seen many species. *Larra melanocnemis* probably belongs in the *anathema* group and it is completely black. In the New World, an all red abdomen predominates in the *bicolor* group although one species has occasional melanic forms. In the other two New World groups the abdomen varies from black to red or a mixture of the two with some species having melanic forms. Color changes may be environmentally induced so the usefulness of color in the phylogeny of *Larra* is limited.

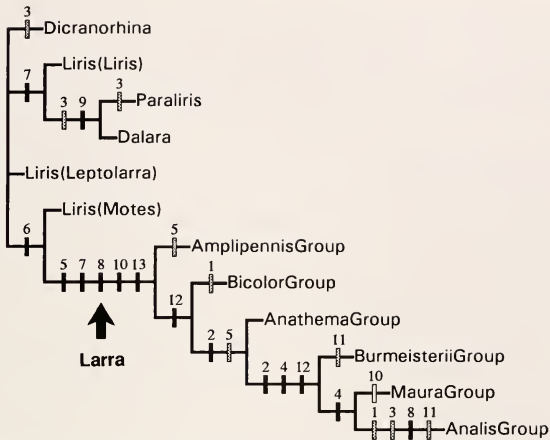
PHYLOGENETIC ANALYSIS AND RESULTS

The characters and taxa summarized in the data matrix (Table 1), were analyzed using the Hennig86 cladistics program (version 1.5) of Farris (1988). Character 8 was run unordered. Character 10 was run with only two states: 0 = female foretibia without spine rows, 1 = foretibia with two or three spine rows. The ie (implicit enumeration) option resulted in 20 equally parsimonious cladograms, with a length of 28, a consistency index of 0.71 and a

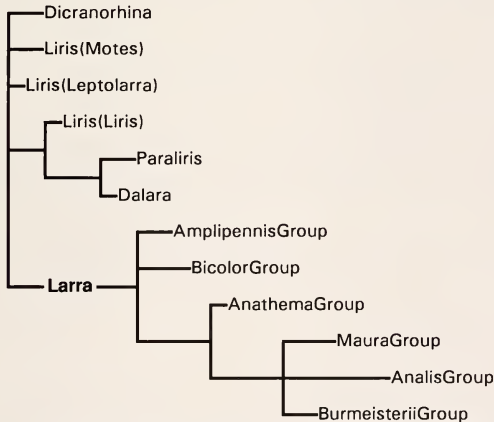
retention index of 0.84. The cladogram reproduced here is representative. The cladogram and strict consensus tree were generated using the Clados program (version 1.0) of Nixon (1991). On the cladogram the black bar represents an apomorphy, the gray bar a parallelism, and the white bar a reversal.

The monophyly of *Larra* was consistently supported in the analysis by five characters (5, 7, 8, 10, 13). *Liris* appears to be paraphyletic and the attempt to resolve the relationships of this genus with the rest of the outgroup and *Larra* explains the numerous cladograms. Within *Larra* branch swapping occurred between the *bicolor* and *amplipennis* groups, and also between the *burmeisterii*, *maura* and *analís* groups. The analysis indicates a reversal of character 10 (female foretibial spine rows) in the *maura* group.

As for the outgroups, no stable set of relationships were found except for the grouping of *Liris* (*Liris*) + (*Paraliris* + *Dalara*), and no group could be reliably determined as the sister group to *Larra*. The strict consensus tree figured here shows the outgroups forming a polytomy with *Larra*.



Representative Cladogram for species groups of *Larra* and related taxa



Strict Consensus Tree for species groups of *Larra* and related taxa

KEY TO FEMALES OF *LARRA*

(Facial measurements should be made at 50X)

1. Pedicel densely setose (Fig. 7); outer foretibial apex not carinate (Fig. 24) 2
- Pedicel asetose or nearly so, at least dorsally (Fig. 8); foretibial apex with short carina on outer face (Fig. 25) 4
2. Submarginal cell II petiolate (Fig. 45) *princeps* (Smith), p. 205
- Submarginal cell II not petiolate 3
3. Pygidial plate broad (Fig. 37), tergum lateral to base of pygidial plate with patch of dense, subappressed setae (Fig. 38); Argentina, Bolivia *stangei* Menke, p. 202
- Pygidial plate narrow (Fig. 35), tergum lateral to base of pygidial plate at most with few scattered setae (Fig. 36); widespread in South America, Central America. *bicolor* Fabricius, p.193 and *praedatrix* (Strand), p. 200
4. Upper interocular distance 0.51-0.56X lower interocular distance (measured tangential to upper edge of tentorial pits), gastral segments I-II red, III-V usually black; southern South America *burmeisterii* (Holmberg), p. 207
- Upper interocular distance 0.32-0.50X lower interocular distance, gaster color variable 5
5. From eastern North America; UID 0.43-0.50X LID *analis* Fabricius, p. 210
- From Central and South America; UID 0.32-0.46X LID 6
6. Pygidial plate narrow (Fig. 67); body 13-20 mm long; face with appressed silver setae between antennal socket and eye margin; thoracic pleura usually dull or weakly shiny; mandible apex often broadly rounded (Fig. 17); Mexico to Uruguay *godmani* Cameron, p. 212
- Pygidial plate broad (Fig. 68); body 7-13.5 mm long; face sometimes without silver setae; thoracic pleura polished; mandible apex narrowly rounded (Fig. 16); South America. *altamazonica* Williams, p. 215

KEY TO MALES OF *LARRA*

(Facial measurements should be made at 50X)

1. Flagellomeres IV-V, III-V or III-VI with placoids dorsally (Figs. 13, 59-62) 2
- Flagellomeres III-XI with placoids dorsally (Fig. 9) 4
2. Upper interocular distance 0.51-0.57X lower interocular distance; gaster black; combined length of pedicel and flagellomere I 0.86-0.96X UID; North America *analis* Fabricius, p. 210
- Upper interocular distance 0.38-0.50X lower interocular distance; gaster red, black, or mixture of both; combined length of pedicel and flagellomere I equal to or greater than UID (if not, gaster is red); neotropical 3
3. Only flagellomeres IV-V with placoids (Fig. 61); mesopleuron and propodeal side polished; South America *altamazonica* Williams, p. 215
- Flagellomeres III-V with placoids (Fig. 60); mesopleuron often dull; Mexico to Uruguay *godmani* Cameron, p. 212
4. Submarginal cell II petiolate (Fig. 45) *princeps* (Smith), p. 205
- Submarginal cell II not petiolate 5
5. Labrum truncate or shallowly concave apically, not downflexed at apex (Fig. 15); volsella uniformly densely setose ventrally from base to apex (Figs. 122-123, 125-126); Argentina, Uruguay, Paraguay *burmeisterii* (Holmberg), p. 207
- Labrum obtusely angular apically, the angulation downflexed (Figs. 16-18); volsellar setation variable, but always sparser or asetose between base of arms and volsellar base (Figs. 70, 74, 77, 82, 90, 110, 117) ... 6

- 6. Ventral surface of volsellar arm of genitalia with very long setae on apical half, abruptly changing to very short setae toward base (best appreciated in lateral view, Figs. 88-91); venter of gonostyle with scattered long setae that do not obscure surface (Fig. 84), or surface partially asetose (Figs. 96-100), or setation consisting of long fringing setae and shorter, denser setae on surface (Fig. 93). *praedatrix* (Strand), p. 200
- Ventral surface of volsellar arm either with shorter setae (Figs. 73-78), or rather densely covered with moderately long setae (Figs. 81-83, 109-110); gonostyle densely, evenly covered with long setae that obscure surface (Figs. 69, 80, 108) 7
- 7. Ventral surface of volsellar arm sparsely covered with short setae that diminish in length basad (Figs. 73-78), shape of volsellar arms typically lyre-like (Figs. 70, 73, 79); widespread in South America *bicolor* Fabricius, p. 193
- Ventral surface of volsellar arm densely covered with moderately long setae (Figs. 109-110), volsellar arms more or less straight (Fig. 109); Argentina, Bolivia *stangei* Menke, p. 202

BICOLOR SPECIES GROUP

Diagnosis.— Male flagellomeres III-XI with placoids (Fig. 9); upper interocular distance in female less than half to more than half length of lower interocular distance (UID 0.44-0.69X LID); transverse sulcus on vertex behind ocelli weakly to moderately impressed at midline; vertex of female head without deep sinus around eye margin (Fig. 3); female clypeus, frons and vertex with considerable dense setation that is often silvery (Figs. 3, 39-40), setae obscuring surface of frons at least laterally (Fig. 39-40); inner surface of female scape densely setose except for narrow asetose zone along anterior (ventral) margin (Fig. 7); female pedicel uniformly setose (punctate) dorsally, the setation less dense than that on flagellomere I (Fig. 34); surface of labrum beveled at free margin or at least sloping down there (Figs. 18, 41), free edge arcuate, angled or lobate; female mandible with long, stout, closely spaced rake setae (Figs. 18-19, 40-41); pronotum anteriorly with transversely elongate sulciform depression at midline, or with two pits (*princeps*) that are narrowly connected; lower edge of smooth, impunctate area at outer apex of foretibia not sharply carinate in female (Fig. 24); outer surface of female foretibia with row of stout, spine-like setae which often is closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one to three stout setae (Fig. 22), male usually with single row of one to four finer setae; inner surface of female forebasitarsus distad of cleaning notch usually with linear asetose zone at least basally (Fig. 27) but entirely setose in one species (Fig. 26).

Included species.— *Larra bicolor* Fabricius, *praedatrix* (Strand), *princeps* (Smith) and *stangei* n. sp.

Discussion.— The numerous placoids of the male flagellum, the setose female scape and pedicel, the strong rake of the female mandible, and the beveled labrum in both sexes, characterize the *bicolor* group. Only the last two are apomorphies and neither is unique to the group. The *bicolor* group has no autapomorphies and it is the least specialized of the three New World groups. Among New World *Larra* only the monotypic *burmeisterii* group shares the male flagellar character, but female features of that group are similar to the *analis* group: inner surface of scape largely asetose, pedicel asetose dorsally, vertex with deep sulcus around eye, female frons largely asetose, and foretibial apex with strong carina that is about one sixth length of tibia. The female mandible of the *bicolor* and *burmeisterii* groups has a well developed rake, differing in that respect from the *analis* group. Although somewhat variable, females in the *bicolor* group have a more extensively and densely setose face, especially the frons, in comparison to the *burmeisterii* and *analis* groups. In the latter two, the frons is usually nearly asetose and polished. The gaster is always red in the *bicolor* group except in some specimens of *princeps* where it may be all black or red and black.

The Old World *amplipennis* group shares some *bicolor* group characters, but the female forebasitarsus is entirely setose within, the female scape is more broadly asetose within, and the labrum is flat to the apex, not beveled there.

The variability of the female forebasitarsus in the *bicolor* group is noteworthy. The inner surface is setose in *stangei* n. sp., similar in this respect to the *amplipennis* group. But the other members of the *bicolor* group have an asetose zone of variable length within species. The asetose zone is never as extensive as it is in the *analis* and *burmeisterii* groups.

Two red-abdomened females that I have studied

are problematical. One was collected at San Bernardino, Paraguay (BERLIN). It has a narrow vertex ($UID = 0.40X$ LID) and the inner surface of the forebasitarsus is entirely setose. This specimen is not *stangei*, the only *bicolor* group species with a setose forebasitarsus. The second female (USNM) was collected at Olinda, Pernambuco, Brasil. It displays a mixture of *bicolor* and *burmeisterii* group characters. As in the latter group the pedicel is asetose and polished, and the forebasitarsus is asetose for most of its length. In other features this specimen agrees with the *bicolor* group: the foretibia lacks an apical carina, the labrum apex slopes downward, the $UID = 0.43X$ the LID, and the pronotum has an undivided dorsal sulcus. The San Bernardino and Olinda specimens may be freaks, or they may represent undescribed species. Only more material will resolve these problems.

The *bicolor* group contains the most commonly collected neotropical species, but after setting aside *princeps*, easily identified by its petiolate second submarginal cell, what remains is a taxonomically very difficult group, the *bicolor* complex. Before I had made a thorough study of the male genitalia, there appeared to be only one species, *bicolor*. Examination of the genitalia of "*bicolor*" males from a number of localities in South America revealed that there was considerable variation in volsellar shape and setation and also density of setation of the gonoforceps. My first thought upon realizing how variable the genitalia were in "*bicolor*" was that it was simply a very plastic species. This hypothesis was enhanced by the fact that females varied also, and I could not find characters that would divide them into two or more "species" reliably. Eventually I dissected every "*bicolor*" male available, nearly 1500 specimens. The result was the recognition of two more species, *praedatrix* and *stangei*. Except for the female of *stangei*, these three cryptic species can be separated reliably only by characteristics of the male genitalia. The females of the two most widespread species, *bicolor* and *praedatrix*, have so far proven inseparable.

In attempting to sort females of the *bicolor* complex to species, I examined the labrum, mandible, clypeus, legs, wings, thoracic sculpture, as well as the features used by Williams (1928). Among the latter are wing color, punctuation of the vertex of the head and form of the transverse depressions behind the ocelli, proportions of basal flagellomeres, comparisons of flagellomere lengths and distance between the eyes at the vertex,

propodeal sculpture including presence or absence of a median carina, and shape of the pygidial plate. Under scrutiny none of these permitted recognition of more than one taxon. The labrum seems highly plastic. Female wing color varies geographically in the *bicolor* complex; they may be pale basally, or entirely infumate. The degree of punctuation of the vertex varies in females from widely scattered pin prick punctures with a few larger punctures sometimes mixed in, to dense, large punctures separated by less than a puncture diameter. The shape of the vertex depressions noted by Williams vary and thus are not useful to separate species. Various head measurements, often diagnostic in wasps, offered no help in the *bicolor* complex. For example, the upper interocular distance varies within these species from less than half to three-fifths the length of the lower interocular distance. The proportions of the basal flagellomeres also vary. The median longitudinal carina of the propodeal dorsum varies from present to absent within species, and propodeal sculpture is variable. The shape of the female pygidial plate is somewhat variable, and the only species in which it appears to be useful at the species level is *stangei*.

Before reaching the conclusion that females of *bicolor* and *praedatrix* were truly inseparable, I examined material that was collected at the same location and date as known males of these species. If females of both species were present, I can only conclude that they are unrecognizable. I had a large sample of *bicolor* complex material from Saavedra, Bolivia in which males of *bicolor* and *praedatrix* were nearly equally numerous, 343 and 304 specimens, respectively. There were 500 females, but I could not separate them into two species. I also studied laboratory reared material from Saavedra sent by Fred Bennett, University of Florida, Gainesville, Florida. He had F1 and sometimes F2 offspring from females and all material was correlated by numbers. Male progeny from the mothers offered positive means of associating males and females of *bicolor* and *praedatrix*. I had hoped that this material would permit detection of characters for separating females of these two species, but such was not the case. All but one of the 14 females proved to be *bicolor* based on male offspring, and the 13 specimens of *bicolor* amply demonstrated how variable the head punctuation and other characters are in that species. Features of the single female of *praedatrix* fell within the variation of *bicolor*.

Larra bicolor and *praedatrix* are largely sympatric in South America and often occur together. The genitalia of *bicolor* vary a little over the range of the species, but variation in *praedatrix* is bewildering (see Figs. 84-107). Further study of *praedatrix* may indicate that it is a complex of cryptic species, but laboratory rearing of material and sophisticated techniques like cuticular hydrocarbon studies may be required to resolve this.

Finally, I have 39 males, all from Venezuela, whose genitalia are fairly similar to *stangei*, a new species from southern Bolivia and northwestern Argentina whose female is fairly reliably separable from *bicolor* and *praedatrix* by the form of the pygidial plate and associated setation. Presumptive females of the Venezuelan taxon are, however, inseparable from those of *bicolor* / *praedatrix*, and it may be that the male genitalia simply represent an extreme variant of *bicolor*. This is another problem for future study.

The absence of female differences poses a critical nomenclatorial problem: the lectotype of *bicolor*, the oldest name, is a female. I have arbitrarily interpreted *bicolor* as the species that was introduced to Puerto Rico and later Florida. The treatment of younger names based on females has also been problematical, and these are discussed under *bicolor* and *praedatrix*.

The species treatments that follow, with the exception of *princeps*, are based largely on male characters because of the female problems discussed above. A composite female description for *bicolor* / *praedatrix* is presented under the *bicolor* treatment that follows.

***Larra bicolor* Fabricius**

Figs. 1, 3, 7, 9-12, 18, 22, 24, 27, 29-36, 39, 69-79

Larra bicolor Fabricius, 1804:221. Lectotype female: "America meridionali" (COPENHAGEN), designated by van der Vecht (1961:17).

Tachytes pagana Dahlbom, 1843:132. Holotype male: "insula St. Croix" (= St. Croix, Virgin Is.) (BERLIN). Synonymy by Patton (1881:389). Type examined by Stadelmann (1897:255).

Larrada americana Saussure, 1867:74. Lectotype male: Caracas, Venezuela (GENEVA), present designation. Synonymy by Patton (1881:389); van der Vecht (1961:17).

Larrada gastrica Taschenberg, 1870:5. Lectotype male: "Paraná", [Brasil or Argentina] (HALLE), designated by Menke (in Bohart and Menke, 1976:238). NEW SYNONYM.

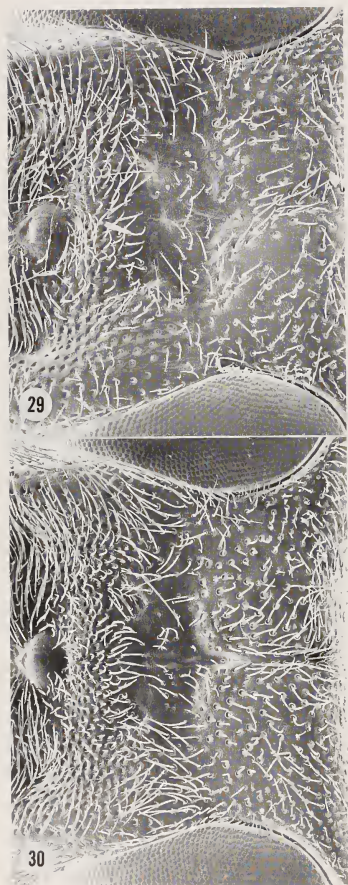
Larra guiana Cameron, 1912:433. Holotype female: Guyana (BMNH). NEW SYNONYM.

Larra scaptesisca Williams, 1928:58. Holotype female: Belém, Brasil (BISHOP). NEW SYNONYM.

Male description.— (951 specimens of which 343 are from Saavedra, Bolivia). Male identifiable only by genitalia: ventral surface of gonoforceps densely covered with uniformly long setae that obscure surface (Fig. 69); ventral surface of volsellar arms sparsely setose, in lateral profile all setae are fairly short although those at apex are longest and there is a gradual shortening of the setae basad (Figs. 75, 78), toward the base of the of the volsellar lobe the setae are restricted to outer area (Figs. 70, 73, 76, 79); in ventral view margins of volsellar arm broadly sinuate, the apex usually acuminate and curving away laterad (Figs. 70, 73, 79); outline of apicodorsal crest of volsellar arm highly variable in lateral profile.

UID0.54-0.73X LID; vertex behind ocelli variably covered by large punctures (Figs. 29-30) that are crowded (separated by a puncture diameter or less), or more widely spaced (separated by 2-4X a puncture diameter, usually unevenly so); transverse impression behind ocelli variable, often forming an angle at midline, the angle often terminating in a pit, sometimes with median sulcus or impression beyond angle that may reach rear edge of vertex; labrum usually arcuate, but free edge occasionally straight, surface of labrum usually impunctate as it slopes down to setose free edge, occasionally slope is punctate. Propodeal dorsum usually with median, longitudinal carina on basal one third or fourth, occasionally extending to apex, sometimes nearly absent. Forewing from base to level of stigma paler (clear to yellowish) than infusate apex; submarginal cell II variable in shape, but very rarely petiolate on marginal cell. Gaster red; tergum VII with or without lateral angle or carina delimiting a pygidial plate; sternum VIII variable, apex notched or rounded. Length 8-14 mm.

Discussion.— The volsella nearly always identifies males of *bicolor*. The somewhat lyre-like form of the two volsellar lobes with their attenuate apices and rather sparse, short setation ventrally are unique. Occasionally the lobes are atypically narrow (Figs. 76, 79), and sometimes the apices are somewhat blunt and not divergent (Fig. 76), but the sparse, short setation is still distinctive. To really appreciate the shortness of the volsellar lobe setation the structure should be viewed in lateral profile (Figs. 75, 78). In the sibling species *praedatrix* the volsellar lobes vary in shape and sometimes resemble those of *bicolor*, but the setae on the apical half are very long and abruptly change to very short setae beyond that point (Figs. 89-91). In *bicolor* the



Figs. 29-30. Vertex of male head of *bicolor* from Puerto Rico showing variation in punctation.

setae gradually shorten from apex to base. Furthermore, the gonostyle in *praedatrix* is never covered densely by the uniformly long setae found in *bicolor*. In *stangei* the volsellar lobes are straight and densely covered ventrally by long setae (Figs. 109-110).

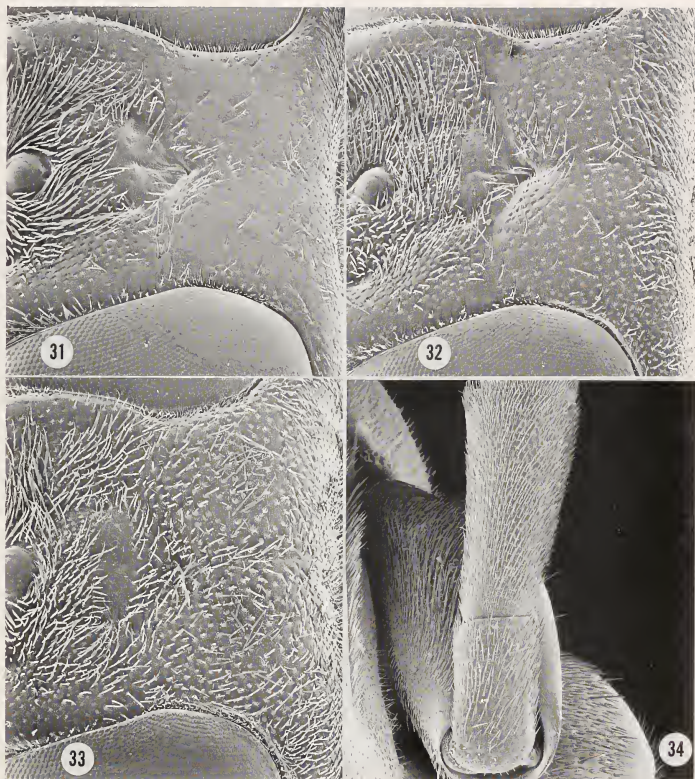
I have 39 males (MARACAY, USNM, FSDA, CORNELL) from several localities in Venezuela (Map 4) whose status is unresolved. The volsellar setation is similar to that of *stangei* (Figs. 81-83), but the lobes are lyre-like as in *bicolor* (Fig. 81), and the gonostyle setation is like *bicolor* (Fig. 80). Putative females of these Venezuelan specimens are not *stangei*. Thus the Venezuelan males may represent a new species, or an extreme variant of *bicolor*. The latter hypothesis is supported by 12 males that I collected in 1985 at Hato Masaguaral south of Calabozo, Venezuela (USNM). Three are typical *bicolor*, ten represent the unresolved taxon, and one has volsellar setation that is somewhat intermediate.

Variation in the upper interocular distance is fairly random geographically, but the shortest UID's occur in the smallest specimens. Likewise, the density of vertex punctation, development of the propodeal carina, etc. are also random. The shape of forewing submarginal cells varies and occasionally the inner and outer veinlets of II meet on the marginal cell. In one male from Paraguay (CSDA) these two veinlets form a very short petiole before reaching the marginal cell.

Female description.— (1158 specimens of which 500 are from Saavedra, Bolivia).

The following descriptive notes apply to females of *bicolor* and *praedatrix* since they are indistinguishable.

UID 0.46-0.63X LID; transverse impression behind ocelli usually deeply, obtusely angular, but occasionally weakly impressed or absent, in the latter a small circular fossa remains where apex of angle would be; vertex punctation varies from very sparse pin prick punctures with scattered larger punctures to very dense macropunctuation (Figs. 31-33); labrum typically flat with deflexed thickened apex (Fig. 18) that varies from impunctate or punctate, sometimes with prominent corners in the latter, outline of free margin highly variable; pronotum with transversely elongate sulciform depression anteromedially (also present in male); propodeal dorsum with median carina of varying length, or carina absent; forewing bicolor (clear basad of stigma) or uniformly infuscate; submarginal cells II and III variable in shape; gaster

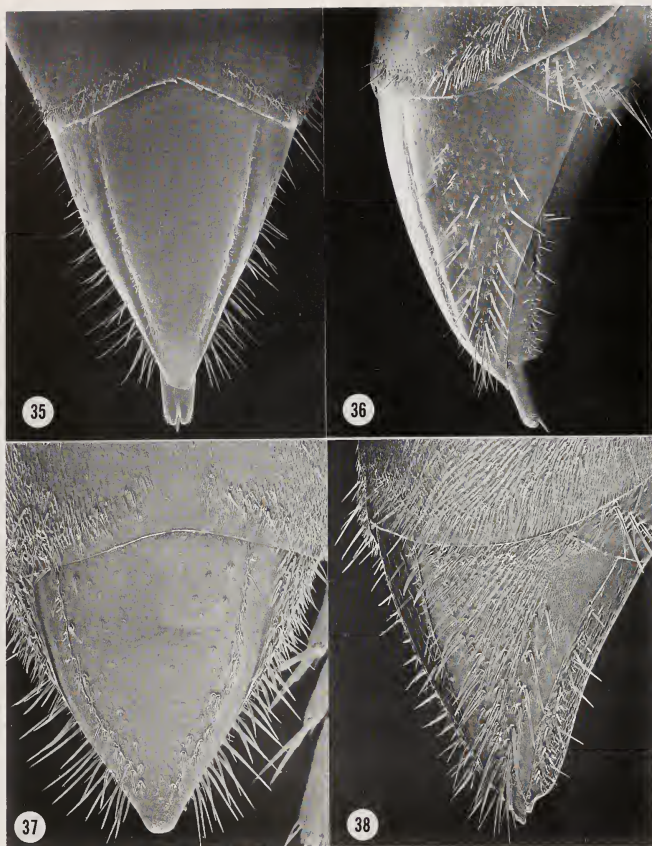


Figs. 31-34. Female head features of *bicolor*. 31-33, Vertex showing punctation behind ocellar triangle. 31, Specimen from Puerto Rico. 32, Specimen from Campinas, Brasil. 33, Specimen from Entre Rios, Argentina. 34, Dorsal surface of pedicel and flagellomere 1.

red except pygidial area blackish in occasional specimens from Argentina; pygidial plate typically narrow, weakly convex (Fig. 35), but rarely broader and nearly like *stangei*; tergum lateral to pygidial plate typically only with scattered, long, erect setae that usually become sparser toward base (Fig. 36), occasionally, however, some shorter, subappressed setae are clustered near base as in *stangei* (some

material from Paraguay). Length: 9.5-20 mm.

Discussion of female variation.— Some variation is geographic. Bicolored wings are typically found only in females from Mexico; El Salvador; parts of Colombia, Peru, Venezuela, and French Guiana; the lower Amazon drainage (east of Santarém in Pará); Puerto Rico; and Florida. Dark wings predominate south of the Amazon Basin, but



Figs. 35-38. Sixth gastral segment of female *Larra*. 35-36, *L. bicolor*. 35, Pygidial plate. 36, Lateral view of right side showing setation. 37-38, *L. stangei*. 37, Pygidial plate. 38, Lateral view of right side showing setation.

material from Guatemala, Costa Rica, Trinidad, the Guianas, and parts of Colombia, Peru and Venezuela usually have evenly infumate wings. The type and density of punctation on the vertex more or less coincides with wing color. Most female

wasps with evenly infumate forewings have dense macropunctuation on the vertex. Exceptions to this rule occur in Venezuela, Trinidad, the Guianas, Peru, Mato Grosso in Brasil, Paraguay and Argentina where the vertex may have sparse pin



prick punctation with scattered larger punctures in dark-winged females. Punctuation intergrades occur everywhere of course. Occasional specimens have a broad pygidial plate or have a cluster of shorter, subappressed setae lateral to it basally, as in *stangei*, but I have not seen specimens with both conditions.

Distribution based on males (Map 1) and females (Map 2).—Widespread in South America: Colombia to about the 38th parallel in Argentina. Also Trinidad, Puerto Rico (introduced) and Florida (introduced). I have seen no males of *bicolor* from Central America, so all the female records from there (Map 2) may pertain to *praedatrix*.

Florida material.—*Larra bicolor* was first liberated at Gainesville, Tampa, and Fort Lauderdale, Florida in 1981 (Hudson et al., 1988). The following year additional releases were made at Bradenton and Lakeland, but the species only became established at Fort Lauderdale. The introduced wasps were collected around Isabella, Puerto Rico. In 1988-1989 Bolivian material of "*bicolor*" from Saavedra was liberated at sites in Alachua County, Florida (Bennett et al., 1990), but according to Fred Bennett (personal communication) the wasps apparently did not become established.

Floridian females have the sparse pin prick punctation on the vertex typical of Puerto Rican material, the latter the offspring of wasps collected originally around Belém, Brasil (Wolcott, 1941). The Fort Lauderdale population has not spread much according to Fred Bennett. I have studied a single female collected at Watson's Hammock, Big Pine Key in Monroe Co., Florida on August 28, 1986 by S. & J. Peck (ALBERTA). This female is puzzling because it has moderately dense punctation on the vertex, and the punctures are intermediate between pin pricks and macropunctuation similar to material from Mexico and parts of Central America. It has bicolored wings just like the Fort Lauderdale material, but the denser head punctation suggests that this female is not offspring from the Fort Lauderdale population. Possibly it represents a chance introduction from Central America or an undetected native population. Positive identification of the Big Pine Key female as *bicolor* will have to await capture of males.

Type notes.—I have not examined the lectotype of *L. bicolor* designated by van der Vecht (1961), but I have studied the material that he compared with it (USNM, LEIDEN). From van der Vecht's (1961) notes and the appearance of his homotypes, it is clear that the lectotype has bicolored forewings ("with faint yellow tinge . . . outer half slightly

darker"). The vertex of the head posterior to the ocelli is very sparsely covered with a mixture of pin prick and regular punctures, the latter far fewer in number. The propodeum has a median longitudinal carina on basal half, and the tegula is amber colored. I am arbitrarily interpreting Fabricius' type as conspecific with the male that I call *bicolor*.

I have examined a male specimen bearing a handwritten label "*Larrada pagana* Dahlb.". The label does not closely resemble the two examples of Dahlbom's handwriting illustrated by Horn and Kahle (1937), but it is similar to the example of Stadelmann's writing in the same work. The locality label on the pin says "Brasilien" which disagrees with Dahlbom's stated origin for the specimen ("ex insula St Crucis dedit Amic. Sommer in Altona mense Julio 1838"). Thus there is doubt about this specimen being the type of *pagana*. On the other hand, *Larra* apparently did not occur in the West Indies until *bicolor* was introduced to Puerto Rico by Wolcott in 1936 (see Wolcott 1936), and I have seen no material from St. Croix or any other Caribbean island except Trinidad. Thus Dahlbom either gave erroneous locality information or his type specimen was mislabeled. In any event, the genitalia of the presumed type of *pagana* are typical for *bicolor*, and I regard Stadelmann's (1897) synonymy as correct.

Saussure's *Larrada americana* was described from three females and a male from Caracas, Venezuela, and a female from "Brasilia". He had an additional female from "Cayenna" that he tentatively treated as a "var.". I have examined the Caracas material, all housed at the museum in Geneva, and the male is a typical *bicolor*; I have labeled it as lectotype. Its genitalia fall within the limits of *bicolor*. The other specimens have not been located.

Taschenberg (1870) described *gastrica* from two males and three females that were taken at three different localities: Paraná, Panda oriental (an area in Minas Gerais, Brasil), and Venezuela. I designated (Menke 1976:238) a male from Paraná as lectotype. I presume that Paraná refers to the state in Brasil, but there is also a city, Paraná, in Entre Rios, Argentina. The genitalia of the lectotype fall within the limits of *bicolor*.

The holotype of *Larra guiana* Cameron is a female with uniformly infumate forewings. The vertex of the head is sparsely covered with a mixture of pin prick and regular punctures, the tegula is amber colored on its posterior half, and the propodeal dorsum has a median carina on its basal third. Cameron's label reads "*Larra guiana* Cameron, Brit.



Guyana", but the name is spelled *guiana* in the original description. Synonymy of *guiana* with *bicolor* is presumptive because the type is a female.

The holotype of *scapteriscica* Williams appears to be only a small example (11.3 mm. long) of *bicolor*, but it could also be *praedatrix*. The vertex punctuation is similar to that described for the types of *bicolor* and *guiana*. But there is no trace of a carina on the propodeal dorsum of the type, or in five of the six topotypical female paratypes, but one of the latter has a long carina. The genitalia of the two topotypical male paratypes are missing unfortunately. Williams' (1928) description and figure suggest that they were not of the typical *bicolor* type.

Larra praedatrix (Strand)

Figs. 84-107

Notogonia praedatrix Strand, 1910:159. Holotype male: Calle S. Miguel, in Asuncion, Paraguay (BERLIN). NEW COMBINATION.

Larra paraguayana Strand, 1910:158. Holotype female: Calle San Miguel in Asuncion, Paraguay (BERLIN). NEW SYNONYM.

Notogonia gastrifera Strand, 1910:160. Lectotype male: Villa Morra, [Asuncion], Paraguay (BERLIN), present designation. NEW SYNONYM, new combination.

Larra pacifica Williams, 1928:55. Holotype female: Bucay, Ecuador (BISHOP). Provisional NEW SYNONYM.

Male description.—(479 specimens, of which 304 are from Saavedra, Bolivia). Male identifiable only by genitalia. Typical form as follows: ventral surface of gonostyle with widely spaced, long setae of variable length, those along the margins longer than most of those on the ventral surface, and increasing in length toward base (Figs. 84-85); ventral surface of volsellar arms sparsely setose, in lateral profile those on apical half very long, abruptly changing to very short setae basad (Figs. 88-91); in ventral view outer margins of volsellar arms straight, the arms converging (Fig. 85).

Variations from this typical form are many (Figs. 92-107), but most share one diagnostic feature, the very long setae on the apical half of the volsellar arm that abruptly change to very short setae beyond; in a few males, however, the long volsellar setae continue all the way to the base of the arm or nearly so (Figs. 92-95).

Sometimes the volsellar arms are much narrowed and straight (Figs. 100-101), or as in *bicolor* they may curve outward somewhat at the apex, but the latter is usually rounded (Fig. 107). The lateral

profile of the volsellar arm crest varies considerably (Figs. 89, 102, 104, 106), and the apex may be sharp (Figs. 88, 94) or rounded (Fig. 107). Most genitalic variants involve gonostyle setation. Sometimes the gonostyle has a narrow asetose zone along the inner margin (Fig. 96). This is often accompanied by an increase in the overall density of setation with setae along the center of the gonostyle being uniformly shorter, sometimes considerably shorter, than those along the margins (Fig. 97). Sometimes the asetose area includes most of the ventral surface of the gonostyle (Figs. 98-100).

UID 0.52-0.73X LID; vertex similar to *bicolor*; labrum usually arcuate but free edge sometimes lobe-like, surface of labrum impunctate as it slopes down to setose free edge, occasionally slope is punctate. Propodeal dorsum without or with median longitudinal carina of variable length. Forewing paler between base and stigma than infusate apex; submarginal cell II not petiolate. Gaster red; tergum VII with or without lateral angle or carina delimiting pygidial plate; sternum VIII variable, apex notched or rounded. Length 7.5-15 mm.

Discussion.—Although there is considerable plasticity in the male genitalia, the volsellar arm setation is usually diagnostic: the setae on the apical half are very long, abruptly changing to very short setae beyond (Figs. 89-91). In some specimens the long setae continue to the base of the arm or nearly so, but they are always restricted to the inner margin of each arm (Fig. 94). Such specimens occur in Costa Rica, and the Brazilian states of Pará, Bahia and Espírito Santo. Occasional specimens of *bicolor* and *stangei* with similar volsellar arm setation have been mentioned under those species treatments, but they have uniformly long, dense setation on the venter of the gonostyle. The occasional males of *praedatrix* with long setae nearly to the volsellar arm base have sparser gonostyle setation characteristic of this species.

Specimens with a narrow asetose zone on the gonostyle (Figs. 96-97) occur in Guatemala, El Salvador, Costa Rica, Colombia, Ecuador, and Argentina. Largely asetose gonostyles (Figs. 98-100) have been noted on specimens from Guatemala, Costa Rica, Bolivia, Mato Grosso and Ceará in Brazil, Paraguay, and Argentina. The great variation in gonostyle setation (Figs. 84, 93, 96-100) is perplexing and there is no correlation with variation in volsellar form and setation. The various volsellar types described and illustrated here occur with most of



the different gonostyles, not just those shown in the SEM figures. There are so many intermediates that I have been unable to identify more than one species. Nevertheless, future work may indicate that *praedatrix* consists of several sibling species. On the other hand, it is still possible that *praedatrix* may prove to be conspecific with *bicolor*. If so, the latter would be an unusually plastic species in terms of male genitalia.

Female.—Indistinguishable from *bicolor*. See that species for particulars.

Distribution based on males (Map 3).—Known from the state of Vera Cruz in Mexico to Buenos Aires Province in Argentina, but apparently mostly absent from the Amazon Basin. *Larra praedatrix* is largely sympatric with *bicolor* in southern South America, but seems to replace the latter species in Central America and the lower slopes of the northern Andes.

Type notes.—Bohart and Menke (1976) incorrectly listed *praedatrix* under the genus *Liris*. Strand's (1910) holotype is a *Larra*, and was probably collected with the females of *paraguayana*; all have similar locality labels. The male genitalia of the holotype of *praedatrix* are identical to figures 84-87.

Strand (1910) tentatively identified two female specimens from Paraguay as *Larra rubricata* Smith, a red abdomened species now placed in the genus *Liris*; he also provisionally named these specimens as "*L. paraguayana*" in the event that they should prove to be distinct from *rubricata*. Strand indicated that the larger specimen was the "Type". The holotype was collected June 10, 1906. I have examined both females and am assuming that the holotype is conspecific with the holotype of *praedatrix*. As first revisor, I have selected *praedatrix* for the name of this species because it is based on a male.

Notogonia gastrifera Strand was described from three males all from the same locality. I have selected and labeled one as lectotype. Its genitalia are of the typical *praedatrix* type. It was collected Nov. 9, 1905; the other two were collected Jan. 3, 1906. Bohart and Menke (1976) incorrectly listed *gastrifera* under the genus *Liris*.

The holotype of *Larra pacifica* Williams is a female from Bucay, Ecuador. His paratypes, all males from Tena, Ecuador, are *praedatrix*. Since I have no authentic males of *bicolor* from Ecuador, but quite a few of *praedatrix*, I am tentatively synonymizing *pacifica* with *praedatrix*.

Larra stangei Menke, new species

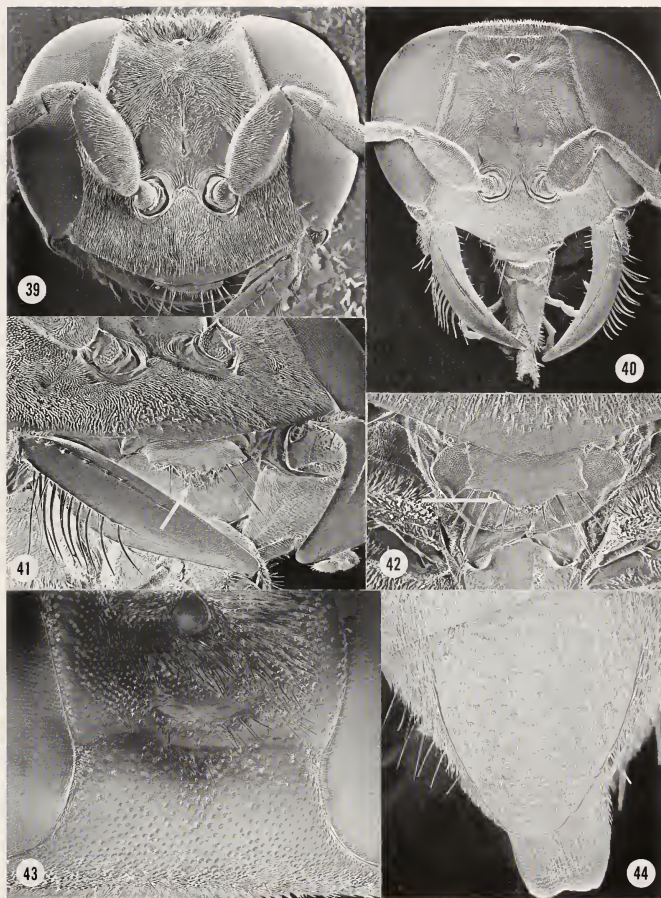
Figs. 19, 26, 37-38, 40-44, 108-111

Description of male.—(11 specimens). Separable from other members of the *bicolor* complex only by genitalia (Figs. 108-111): ventral surface of gonostyle densely covered with uniformly long setae that obscure surface (Fig. 108); ventral surface of volsellar arms densely, uniformly covered with long setae (Fig. 109); in ventral view, outer margin of volsellar arm straight (Fig. 109); apicodorsal crest of volsellar arm not or only slightly incurved in dorsal view.

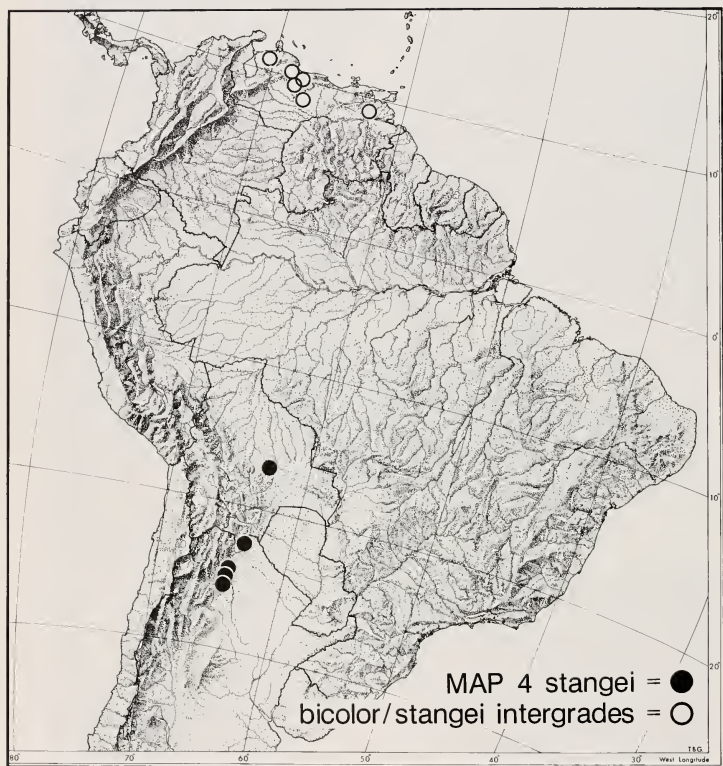
UID 0.63-0.69X LID. Vertex behind ocelli with transverse impression that does not form an obtuse angle at midline, macropunctate, punctures nearly contiguous. Labrum impunctate, surface smoothly sloping down to free margin. Median longitudinal carina of propodeal dorsum sometimes absent, but usually extending to apex. Wings uniformly infumate in Argentine specimens, forewing bicolored and hindwing largely pale in Bolivian material; second submarginal cell of forewing not petiolate. Gaster red; tergum VII with broad, flat pygidial plate delimited by sharp lateral carinae (Fig. 44); sternum VIII with shallow apical V-notch (Fig. 44). Length 11-14 mm.

Female.—(17 specimens). UID 0.53-0.57X LID; transverse impression behind hindocelli obtusely angular, vertex densely bipunctate, macropunctures much more numerous (Figs. 43); surface of labrum flat, sharply truncate apically, free edge thickened and forming prominent deflexed lobe (Figs. 41-42); pronotum anteriorly with transversely elongate sulciform depression at midline (also present in male); inner surface of forebasitarsus without asetose zone distad of cleaning notch (Fig. 26); propodeal dorsum with or without median, longitudinal carina; gaster red, tergum VI with broad pygidial plate that is flat on apical half, and whose margins are cariniform on apical half (Fig. 37), surface of tergum lateral to plate apex with many long, stiff setae that become shorter, denser and more appressed toward base (Figs. 37-38); wings uniformly infumate in Argentine specimens, forewing bicolored and hindwing largely pale in Bolivian specimens. Length 13.5-18.5 mm.

Discussion.—The densely setose volsella is the most diagnostic male feature of *stangei* although some male *Larra* from Venezuela have similar genitalia. In the Venezuelan material, however, the volsellar lobes curve outward apically in ventral



Figs. 39-44. Features of *bicolor* group. 39-40, Female face. 39, *bicolor*. 40, *stangei*. 41-42, Labrum and associated structures in female of *stangei*. 41, Oblique view of mandible and labrum (arrow points to deflexed apical lobe of labrum). 42, Closeup of labrum. 43, Female vertex of *stangei* showing ocelli and postocellar punctation. 44, Male tergum VII showing pygidial carinae, apex of sternum VIII visible below.



Smithophorus Smithsonian, 1983
Prepared by Theophilus Berri Gresswell

view (Fig. 81), just as in *bicolor*, and these specimens may be variants of that species and not *stangei* (see *bicolor* treatment). The broad, flat female pygidial plate of *stangei* is distinctive in this sex (Fig. 37), but by itself is unreliable because of variation in this structure in *bicolor/praedatrix*. Usually, however, the latter do not have short, dense, subappressed setae on the side of the tergum (Fig. 38), or if they do, the plate is narrow. In older, worn female specimens of *stangei* the subappressed setae may be abraded, but their pits are still visible. The absence of a clearly demarked asetose zone on the forebasitarsus (Fig. 26) is another apparent character of females of *stangei*, but in view of the variation in the development of this zone in the other species of the group, and the small sample size for *stangei*, the reliability of this character is unknown.

Two males from Rosario de Lerma, Salta, Argentina (CSDA, FRITZ) have puzzling genitalia. In one the volsella has long setae along the inner part of each arm from apex to base, but they are not as dense as in *stangei*, and laterally the setae are shorter. The apicodorsal crest of the volsellar arm is somewhat higher than the average condition in *stangei*, and it curls inward strongly in dorsal view. In the other specimen the volsellar setation is typical of *stangei* but the volsellar arm is constricted subapically and the apicodorsal crest is sinuate and incurved. In view of the genitalic variation in other species, these two specimens probably are *stangei*, but I have not included them among the paratypes. Curiously a third male collected at the same place is a typical *bicolor* (CSDA).

Etymology.— I take pleasure in naming this wasp after my long time friend, Lionel Stange, who collected nearly half of the known material.

Distribution (Map 4).— Northwestern Argentina, southern Bolivia.

Types.— **Holotype male:** BOLIVIA, Santa Cruz: Sand dunes at El Palmar Oratorio, about 40 kms southeast of Santa Cruz, Jan. 25, 1980, Lionel A. Stange (FSDA). **Paratypes:** BOLIVIA, Santa Cruz: same data as holotype, 5 males, 4 females, L. A. Stange (FSDA, USNM); Santa Cruz, one male, Feb. 10, 1971, M. Fritz (FRITZ). ARGENTINA, Salta: Alemania, one male, five females, Feb./Mar. 1983, M. Fritz (FRITZ); La Viña, one male, three females, Dec., Feb. 1983-1984, M. Fritz, M. Wasbauer (FRITZ, CSDA); Tartagal, two males, three females, Nov. 1971, M. Fritz (FRITZ); Guachipas, one female, Feb. 1989 (FRITZ); Coronel Moldes, one female, Feb. 1990 (FRITZ).

Larra princeps (Smith)

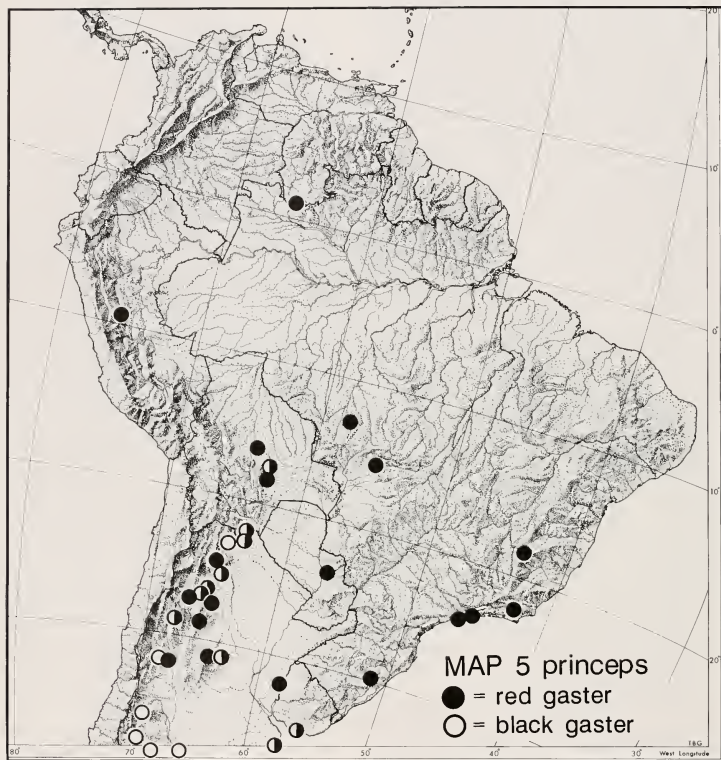
Figs. 45-46, 112-119

Larraxena princeps Smith, 1851:30. Lectotype female: "Brazil" (BMNH), present designation.

Description.— (126 males, 124 females): Male UID 0.50-0.62X LID; female UID 0.44-0.50X LID (as measured tangential to upper edge of antennal sockets). Male vertex behind ocelli with transverse impression that is usually deeply, triangularly depressed at middle; deep groove often extending posterad from apex of this depression; macropunctate, punctures nearly contiguous to one diameter apart. Female vertex similar except no groove extending posterad from triangular depression and punctures varying from fine to coarse and often separated by 2 or 3 puncture diameters. Labrum impunctate in both sexes, surface smoothly sloping down to free margin that has a few marginal punctures. Pronotum anteriorly with pair of oval pits that are usually narrowly connected. Propodeal dorsum carina usually extending nearly to apex, but sometimes much shorter or even absent. Wings evenly infumate with rare exceptions; second submarginal cell petiolate on the marginal cell (Fig. 45), petiole rarely very short or absent (Fig. 46). Gaster black or red, sometimes red with black areas at tergal and sternal margins; female tergum VI and pygidial plates same as *bicolor*; male tergum VII without pygidial carinae; male sternum VIII variably emarginate apically; ventral surface of gonostyle uniformly covered with dense, long setae that obscure surface (Fig. 112); volsellar arms broad, densely covered with long setae ventrally that obscure surface (Figs. 112, 116-117); apicodorsal crest of volsellar arm not incurved in dorsal view (Fig. 118). Males 9-16 mm long, females 13-20 mm. long.

Discussion.— The petiolate second submarginal cell immediately identifies *princeps*. I have seen two Argentine females in which the cell is not petiolate on one wing (Fig. 46), so it is likely that rare individuals might have non-petiolate cells in both wings. Separation of them from *bicolor/praedatrix* should be possible by the presence of two pronotal pits. The male genitalia of *princeps* are fairly uniform and quite distinctive, particularly the broad volsellar arms that are densely covered with setae (Figs. 116-117).

Larra princeps is the only species in the *bicolor* group that has two color forms. All black specimens



occur mainly in the southern part of the species' range, but both color morphs occur together especially along the eastern side of the Andes in Argentina (Map 5). Red morphs predominate, however. Exceptions to the darkly infumate wings occur in Peru and Entre Rios Prov. in Argentina where the wings are paler toward the base and the infumation is less dense.

*Distribution (Map 5).—**Larra princeps* is a commonly collected species in Argentina, but the species appears to have a fairly wide distribution in South America based on a few scattered records in Peru, Venezuela and Brasil.

Type notes.— I have examined the two female syntypes described by Smith in 1851. Both have a red abdomen and typical wing venation. I have

placed my lectotype label on the specimen that already had a circular "type" label.

BURMEISTERII SPECIES GROUP

Diagnosis.— Male flagellomeres III–XI with placoids; upper interocular distance in female at least half length of lower interocular distance; transverse sulcus on vertex behind ocelli weakly to moderately impressed at midline; vertex of female head usually with narrow, deep sinus around eye (Fig. 49); female frons beneath transverse swelling polished, nearly impunctate and largely asetose except at level of antennal sockets, clypeus laterally, and vertex (Fig. 47); inner side of female scape largely asetose, with only few scattered setae basally (Fig. 48); female pedicel asetose dorsally and ventrally, polished, at most with a few scattered setigerous punctures (Fig. 48); labrum flat, at most narrowly downflexed at midapex (Fig. 15); female mandible with numerous long, stout rake setae (Fig. 15); pronotum anteriorly with pair of oval pits at midline; lower edge of smooth, impunctate area at outer apex of female foretibia margined by sharp carina that extends about one sixth tibial length (Fig. 51), male with much shorter carina; outer surface of female foretibia with row of stout, spine-like setae that often is closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one or two stout setae (Fig. 50), male usually with single row of one or two fine setae; inner surface of female forebasitarsus distad of cleaning notch with asetose linear zone that extends to apex (Fig. 52).

Included species.—*Larra burmeisterii* (Holmberg).

Discussion.— This group displays a curious mixture of characters. The male has a plesiomorphic antenna just like the *bicolor* group. The female, however, shares several apomorphic features with the *analis* group (asetose pedicel, asetose inner surface of scape, frons largely asetose and polished, sinus present around upper margin of eye, and carinate foretibial apex). The ocular sinus is not as pronounced as in the *analis* group and it represents an intermediate condition. The upper interocular distance in the female of *burmeisterii* is broader than in the *analis* group.

Apomorphies of the *burmeisterii* group include the shiny, asetose female pedicel, the female ocular sinus, the shiny asetose and nearly impunctate female frons, the moderately well developed female mandibular rake setae, the pair of pronotal pits, the

foretibial carina in both sexes, and the asetose linear area on the inside of the female forebasitarsus. None are unique to the group.

The female pedicel of the Old World species *anathema* (Rossi), the type species of *Larra* , approaches the condition found in *burmeisterii* . It is polished dorsally but the surface is sparsely setose, and the outer and ventral surfaces are densely setose. The inner surface of the female scape of *anathema* is polished and largely asetose just as in *burmeisterii* . The female of *anathema* lacks a deep sinus around the upper margin of the eye, the foretibial carina is absent, and the forebasitarsus has only a vaguely defined asetose area basally. Both sexes of *anathema* have a flat labrum just like *burmeisterii* , however. The Australian *L. melanocnemis* Turner, which probably belongs in the *anathema* group, shares most of the latter's features but the female forebasitarsus has a distinct asetose zone.

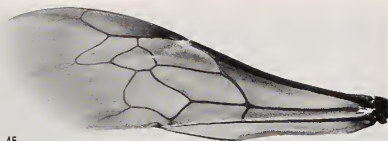
The gaster in *burmeisterii* may be red, black or combinations of both colors.

Larra burmeisterii (Holmberg)

Figs. 15, 47–52, 120–127

Larrada burmeisterii Holmberg, 1884:221. Holotype female: Colonia, Paraguay (destroyed).

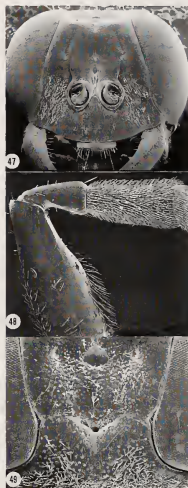
Description.— (72 males, 183 females): Male UID 0.60–0.66X LID; female UID 0.51–0.56X LID (as measured tangential to upper margin of tentorial pits). Male vertex behind ocelli with weakly to strongly impressed angular depression at midline posterior to which is a narrow, linear impunctate zone; macropunctate, punctures about a diameter apart or less. Female vertex with strong angular depression behind ocelli, and sometimes with narrow, linear impunctate zone posterior to it, this area often somewhat elevated even if punctate; punctures nearly contiguous posteriorly but becoming sparser toward transverse impression, sometimes impunctate and polished next to it (Fig. 49). Labrum scarcely projecting beyond clypeus, especially in male, polished, impunctate, flat to free margin although sometimes indented there at midline, apex slightly arcuate, truncate or shallowing emarginate (Figs. 15, 47). Propodeal dorsum carina present and of variable length, or more frequently absent. Wings darkly infumate in female, clear or weakly infumate in male; second submarginal cell of forewing not petiolate. Male



45



46



Figs. 45-46. Left female forewing of *Larra princeps*. 45, Wing with normal petiolate second submarginal cell. 46, Wing with aberrant second submarginal cell (right wing is normal).

Figs. 47-49. *Larra burmeisterii*, features of female head. 47, Face. 48, Inner side of scape, pedicel and flagellomere I of left antenna. 49, Vertex.

abdomen all red or all black, but sometimes first two or three segments are red, the remainder black; female abdomen sometimes all red, but usually segments I-II and VI red, III-V black, or occasionally segments I-III red, remainder black; female tergum VI and pygidial plate similar to that of *bicolor*; male tergum VII usually with pygidial carinae, sternum VIII usually notched apically but sometimes entire; ventral surface of gonostyle densely covered with long setae that obscure surface (Fig. 120), volsellar arm of uniform width to rounded apex (Fig. 124), or constricted subapically (Fig. 121), entire venter of volsellus densely covered with long setae (Figs. 121-126); apicodorsal crest of volsellar arm variable in lateral profile (Figs. 123, 126). Males 8.5-13.5 mm long, females 11-18.5 mm long.

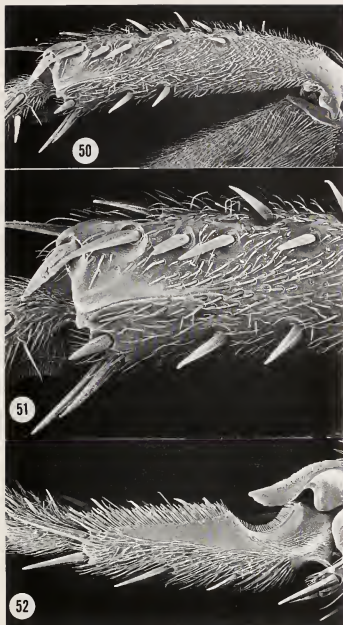
Discussion.—The male of *burmeisterii* is reliably identified only by genitalic characters, primarily the completely setose volsella (Figs. 122-123, 125-126). The flat, non-beveled labrum is useful, but often the labrum is concealed in dead material. The female can be identified by the polished, nearly

asetose pedicel and the broad upper interocular distance (equal to at least half the lower interocular distance). Color is also useful. No other species within the range of *burmeisterii* has a bicolored abdomen, but some specimens have an all red or all black gaster. The ocular sinus varies. In some females it is barely evident.

Males with a completely black gaster come from the provinces of Rio Negro, Buenos Aires, Entre Rios and Corrientes. Females with an all red gaster occur in the Argentine provinces of Rio Negro, Buenos Aires, Mendoza, and Tucuman as well as in Uruguay. Bicolored forms are known from all but Rio Negro and Tucuman, however.

Distribution (Map 6).—*Larra burmeisterii* is widespread in Argentina and Uruguay, and occurs as far south as the Rio Negro. I have a single record from Paraguay, and several from Rio Grande do Sul in southernmost Brasil. I have seen a single female labelled Santiago, Chile (VIENNA) but I presume that this is erroneous.

Type notes.—The holotype was destroyed by



Figs. 50-52. *Larra burmeisterii*, features of female foretibia and tarsus. 50, Outer surface of tibia. 51, Outer apex of tibia showing carina. 52, Inner surface of basitarsus.

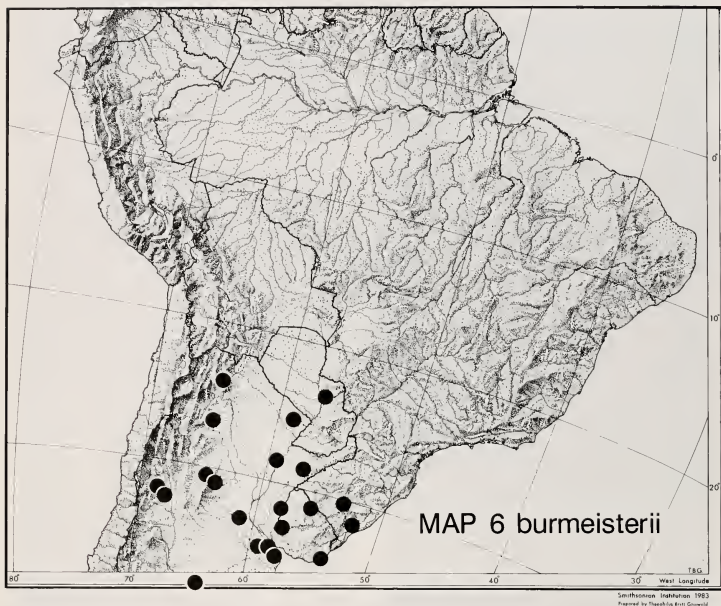
museum pests long ago, but Holmberg's (1884) description is sufficient to identify the species. The first three gastral segments were red in the type, the remainder black. This agrees with some of the females that I have seen from Uruguay. Although Holmberg used a Lynch Arribalzaga ms. name, *burmeisterii*, the description is Holmberg's. Apparently Lynch Arribalzaga was preparing a revision of the Argentine "*Larrada*" but it was never published.

ANALIS SPECIES GROUP

Diagnosis.— Placoids restricted to male flagellomeres III-VI (Figs. 13, 59-62); upper interocular distance of female less than half length of lower interocular distance (UID 0.32-0.46X LID); transverse sulcus on vertex behind ocelli usually deeply impressed at midline; vertex of female head with broad, deep sinus around eye (Figs. 4, 63-65), male with shallower sinus; female frons beneath transverse swelling polished, variably punctate, largely asetose except at level of antennal sockets, clypeus laterally, and vertex (Figs. 2, 53); inner surface of female scape largely asetose except at base (Fig. 8); female pedicel almost entirely asetose (only a few scattered setae), surface smooth, polished (Fig. 8); female mandible with poorly developed rake, setae scattered, weak (Figs. 16-17, 56, 58); labrum beveled or sloping down at apex to obtusely angular or arcuate free margin (Figs. 16-17, 55-58); pronotum anteriorly with pair of oval pits at midline that sometimes are narrowly connected; lower edge of smooth, impunctate area at outer apex of female foretibia margined below by sharp carina that extends about one-sixth tibial length (Fig. 25), male without carina; outer surface of female foretibia with row of stout spine-like setae that is occasionally closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one to three stout setae (Fig. 23), male usually with single row of one to four finer setae but sometimes absent; inner surface of female forebasitarsus distad of cleaning notch with asetose linear zone that extends to apex (Fig. 28). Propodeal dorsum usually without median longitudinal carina, or with only a remnant, but occasional specimens have complete carina. Male tergum VII without pygidial carinae. Male genitalia essentially identical in all species: ventral surface of gonostyle densely covered with long setae (Fig. 128); volsellar arms straight, broadening distally, ventral surface with long setae (Fig. 129); apicodorsal crest of volsellar arm sinuate in dorsal view (Fig. 130).

Included species.— *Larra altamazonica* Williams, *analisis* Say, and *godmani* Cameron.

Discussion.— The presence of placoids on just a few of the basal male flagellomeres is an autapomorphic feature of the *analisis* group. In all other *Larra* placoids are found on flagellomeres III-XI. In the female, the combination of a polished, impunctate pedicel, the narrow upper interocular distance (less than 0.50X LID), the deep impression at the midline of the vertex, and the deep sinus around the upper eye margin, and the weak mandibular rake set the *analisis* group apart from other New World *Larra*, but of these apomorphies,



only the weak mandibular rake is unique to the group. Females of the Old World *maura* species group share the other apomorphies, but the outer face of the foretibia in that assemblage has no spine rows or an apical carina, and the labrum is flat, without an apical bevel. The female frons in the *maura* group apparently is always asetose and is essentially impunctate beneath the transverse swelling, a trait shared with one species of the *analisis* group, *altamazonica*. In the other two species of the *analisis* group, the frons, though shiny, is clearly punctate.

Species characters are few in this group. The number of flagellomeres with placoids is useful in males, but there is some intraspecific variation. Unfortunately, male genitalia seem identical in the three species. Because of this, identification of occasional males of *altamazonica* and *godmani* with atypical antennal placoid distribution can be

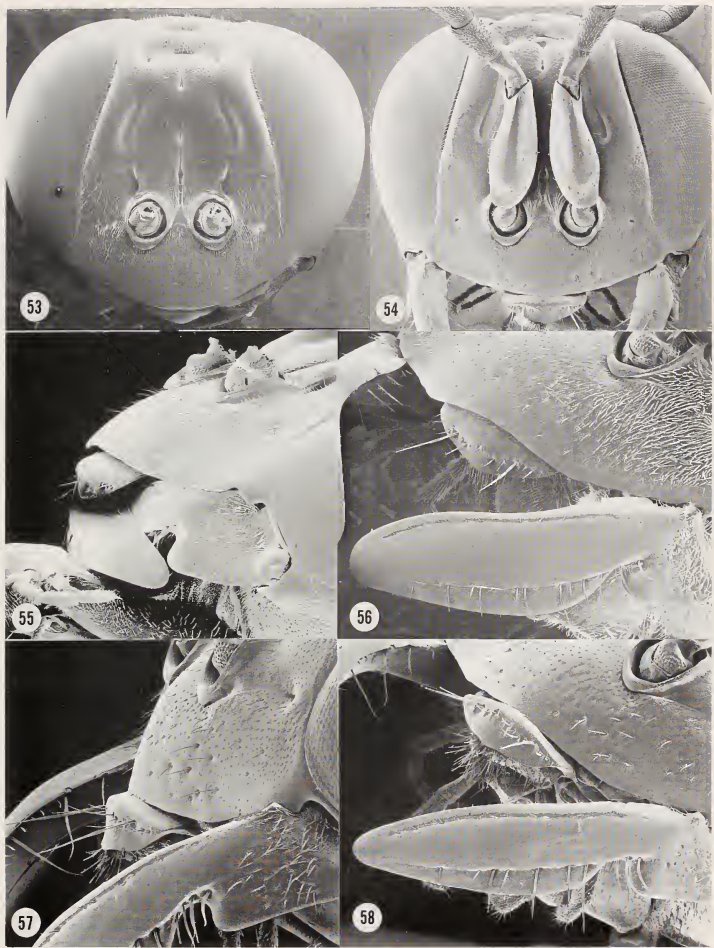
problematical. The length of the UID in relation to the LID is useful to some extent in both sexes, but there is some overlap between species. The shape of the female pygidial plate is diagnostic for *altamazonica*. Color in the *analisis* group is constant in *analisis*, but *altamazonica* and *godmani* have forms with a black gaster, and forms with a red gaster, or combinations of both.

Larra analis Fabricius

Figs. 13-14, 53, 55, 59, 63, 66, 128-131

Larra analis Fabricius, 1804:220. Holotype female: Carolina. (PARIS). Type studied by van der Vecht (1961:17).

Larrada canescens Smith, 1856:292. Holotype male ("female"): Georgia. (BMNH). Synonymy by R. Bohart (in Bohart and Menke, 1976:237).



Figs. 53-58. Female head features in *analis* group. 53-54, Face. 53, *analis*. 54, *altamazonica*. 55-58, Clypeus, labrum and mandible. 55, *analis*. 56, *godmani*. 57-58, *altamazonica*.

Larrada americana Cresson, 1872:214. Holotype male: Texas [presumably Bosque Co.]. (ANSP). Junior secondary homonym of *Larra americana* Saussure, 1867. Synonymy by G. Bohart (1951:953).

Larra cressonii Fox, 1894:482. New name for *americana* Cresson.

Description.— (181 males, 273 females): Male UID 0.51-0.57X LID; female UID 0.43-0.50X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by about one diameter on disk, closer peripherally; female vertex punctures similar to male, but sometimes 3 or 4 diameters apart discally (Fig. 63); female frons finely punctate; placoids present on male flagellomeres III-V, and sometimes VI, lengths of placoids variable on III and VI (Figs. 13, 59); surface of labrum gradually curving down to free margin in male, more sharply beveled in female (Fig. 55); apex of female mandible narrowly rounded (Fig. 55). Pronotal pits narrowly connected. Mesopleuron dull or weakly shining. Wings evenly, darkly infumate. Propodeal dorsum usually delimited posterad by transverse carina. Male gaster black, terga sometimes with silvery apical fasciae; female gastral segments I-III black, IV-VI red. Male sternum VIII rounded at apex, often indented there; female pygidial plate narrow (Fig. 66). Male 8.5-14.5 mm long, female 12.5-18.5 mm long.

Discussion.—*Larra analis* is the only Nearctic species and it has a non-varying color pattern that permits easy identification. Males are all black and females have a black gaster with the last three segments red. Occasional melanic females of *godmani* from South America have the last three segments of the gaster red and thus resemble *analis*, but the UID is narrower in the latter species. The UID in melanic *godmani* ranges from 0.32-0.39X the LID, while the UID in *analis* ranges from 0.43-0.50X the LID. Males of *analis* generally have a broader UID than either *godmani* or *altamazonica*. In *analis* the UID is 0.51-0.57X the LID. In the other two species the male UID ranges from 0.35-0.50X the LID.

Distribution (Map 7).— Widespread in the eastern United States from about the 104th meridian to the southern and eastern coasts. Northward *analis* apparently does not extend beyond the 43rd parallel, Livingston Co. in Michigan and Taunton, Massachusetts being the northernmost records seen. The wasp is evidently uncommonly collected except in the southern tier of states.

Type notes.— J. van der Vecht (1961), R. Bohart (in Bohart and Menke, 1976), and G. Bohart (1951)

studied the types of *analis*, *canescens*, and *americana*, respectively, and I accept their interpretations. Cresson (1872) described *americana* from a single male which is now in Philadelphia (see Cresson, 1916). Thus the male in the U. S. National Museum of Natural History collected by Belfrage in Texas and labeled as "type" is a pseudotype.

Larra godmani Cameron

Figs. 4-6, 17, 23, 25, 28, 56, 60, 64, 67

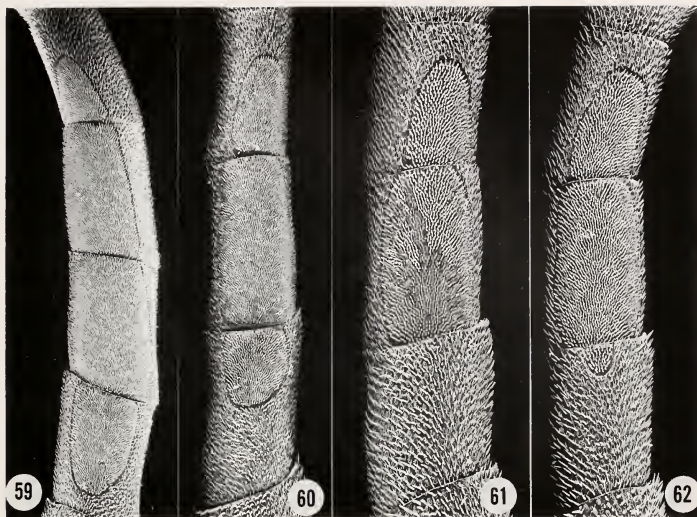
Larrada aethiops Smith, 1873:56. Lectotype female: "St. Paulo" (=São Paulo de Olivença, Amazonas) Brasil (BMNH), present designation. Junior primary homonym of *Larrada aethiops* Cresson, 1865.

Larra godmani Cameron, 1889:49. Lectotype female: Orizaba, Mexico (BMNH), present designation. NEW SYNONYM.

Larra braunsii Kohl, 1898:351. Lectotype female: Santos, Brasil (State of São Paulo) (VIENNA), present designation. NEW SYNONYM.

Larra transandina Williams, 1928:56. Holotype female: Tena, Ecuador (BISHOP). NEW SYNONYM.

Description.— (290 males, 186 females): Male UID 0.35-0.50X LID; female UID 0.32-0.46X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by less than a diameter to more than a diameter on disk, closer peripherally; female vertex irregularly punctate, punctures scattered, less than diameter apart to several diameters apart, punctures sometimes very fine, almost pinprick-like and widely separated, the vertex almost impunctate (Fig. 64); female frons finely punctate, occasionally almost impunctate; placoids typically present on male flagellomeres III-V (Fig. 60), flagellomere III rarely without placoid, placoid on III usually occupying apical half, that on V usually occupying basal two thirds or more; surface of labrum gradually curving down to free margin (Figs. 17, 56); apex of female mandible broadly rounded (Figs. 17, 56) or narrowly rounded. Pronotal pits separate. Mesopleuron usually dull or weakly shining, infrequently shiny. Wings darkly infumate, except sometimes paler at base. Propodeal dorsum sometimes delimited apically by transverse carina. Gaster all red or all black (19% of male and 17% of female specimens melanic), occasional red male specimens have tergum I suffused with black, occasional black specimens of both sexes have last two or three segments red. Male sternum VIII with apical emargination, or rounded and/or weakly



Figs. 59-62. Male flagellomeres III-V or VI showing placoids. 59, *analisis*. 60, *godmani*. 61, *altamazonica* (typical). 62, *altamazonica*.

notched. Female pygidial plate narrow (Fig. 67). Males 8-13.5 mm long, females 13-20 mm long.

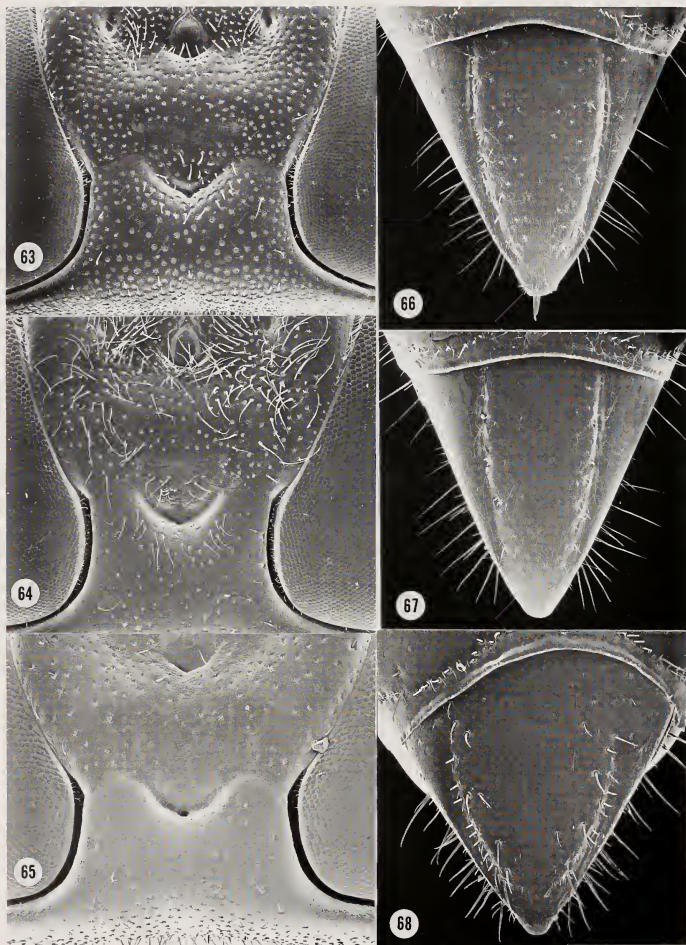
Discussion.— The presence of placoids on male flagellomeres III-V of *godmani* differentiates the species from males of *altamazonica*. But I have seen one red gastered specimen of *godmani* without a placoid on flagellomere III (Darién, Panamá (Quintero). Positive identification of such specimens can be problematical. In the case of the Panamanian wasp, a typical male was taken at the same time and place, thus verifying its identity as *godmani*. Also it has rather dull mesothoracic pleura typical of *godmani*. I have also seen two melanic males without a placoid on flagellomere III (FSDA, MCZ) that I regard as *godmani* based on body length and rather dull mesothoracic pleura.

The shape of the female pygidial plate (Fig. 67) is the most reliable character for separating *godmani* from *altamazonica*. The latter species has a broader plate (Fig. 68). The frons below the transverse swelling is usually very finely punctate in females, at least in part. In *altamazonica* the female frons is

nearly impunctate or the punctures are largely effaced. The thoracic pleura of *godmani* are duller compared to *altamazonica* which tends to have shiny pleura.

Males of *godmani* with an all red gaster are quickly separated from males of *analisis*, all of which have a black gaster. The narrower male UID of *godmani*, especially those with an all black gaster, generally distinguishes this sex from *analisis*. The UID ranges from 0.35-0.43X the LID in black males of *godmani*, while in *analisis* the range is 0.51-0.57.

Females with a red gaster are easily separated from *analisis*, but the occasional melanic *godmani* with the terminal segments red must be identified by measuring the upper interocular distance. In melanic *godmani* the UID ranges from 0.32-0.39X the LID; in *analisis* the UID is 0.43-0.50X the LID. Of course the two species are allopatric. In about half of the *godmani* females studied, the apex of the mandible is more broadly rounded than in *analisis* or *altamazonica* (compare Figs. 56, 58), but in all material studied from Mexico, the northern end of the



Figs. 63-68. Female features of *analis* group. 63-65, Vertex of head. 63, *analis*. 64, *godmani*. 65, *altamazonica*. 66-68, Pygidial plate. 66, *analis*. 67, *godmani*. 68, *altamazonica*.

species' range, the mandible is more or less narrowly rounded apically.

All black males represent about 20% of my material, but all specimens from Central America and Mexico have a red gaster. Black males occur randomly in South America north of the Tropic of Capricorn. I have seen only one melanic male from south of the 23rd parallel, and it is an old specimen labeled "Montevide.", presumably Montevideo, Uruguay (BERLIN). Occasional black males from Colombia, Ecuador, Peru and northern Brasil have the last two or three gastral segments red.

All black females occur less frequently (17%) than males but like them all are from South America. They occur randomly from Venezuela down to Bolivia, and Mato Grosso, Brasil, and along the Amazon River in Brasil. I have not seen melanic females south of the 18th parallel, nor from Trinidad and the Guiana's. I have seen red tipped black females from Venezuela, Colombia, Ecuador and Pará, Brasil. The upper interocular distance in melanic females tends to be narrower than in bicolored ones. The UID ranges from 0.32-0.39X the LID in melanics, and between 0.33-0.46 in bicolored females.

I have one small female from Leticia, Colombia (FSDA) that I have identified as *godmani*; it is only 9 mm long. It has a narrow pygidial plate, but the pleura are shiny like *altamazonica*. Its UID is 0.44X the LID which is beyond the range of female *altamazonica*.

Distribution (Map 8).—Widely distributed in the Neotropical Region, ranging from just south of the Tropic of Cancer in Mexico to extreme northern Argentina, Paraguay, southeastern Brasil and Uruguay. Bolivian material of *godmani* was liberated in Alachua Co., Florida in 1988-89 under the name *braunsii* (Bennett et al., 1990), but the species apparently did not establish.

Type notes.—Smith described *aethiops* from an unspecified number of females from "St. Paulo" and "Ega", Brasil that had a black gaster. I have examined four syntypes, one labelled St. Paulo and three labelled Ega (BMNH, OXFORD). I have selected the São Paulo de Olivença female as lectotype and so labelled it. The mandible apex is broadly rounded in the four specimens, and the UID is 0.34X the LID in the lectotype.

Cameron had at least two red abdomened females from Orizaba, Mexico when he described *godmani*. I have studied two from the BMNH and placed a lectotype label on the best specimen (its gaster is glued to a card). The mandible apex is not broadly rounded in either specimen. The UID is 0.36X the LID in the lectotype.

Kohl described *braunsii* from three female syntypes (VIENNA) with a red gaster. I have studied them and selected the specimen from Santos, Brasil as lectotype. Only the Pebas, Peru ("Pevas") syntype has the mandible apex broadly rounded. The UID is 0.40X the LID in the lectotype.

Williams female holotype of *transandina* has a red gaster, the mandible apex is broadly rounded and the UID is 0.38X the LID.

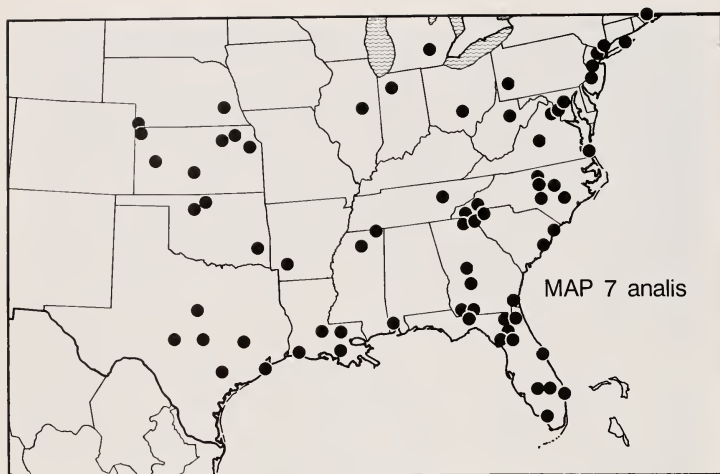
Larra altamazonica Williams

Figs. 2, 8, 16, 54, 57-58, 61-62, 65, 68

Larra altamazonica Williams, 1928:57. Holotype female: Tena, Ecuador (BISHOP).

Description.—(42 males, 50 females): Male UID 0.40-0.49X LID, female UID 0.37-0.41X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by less than diameter to two or three diameters on disk, denser peripherally; female vertex punctures often pin prick-like, punctation usually absent laterally, punctures sparse on disk, usually several diameters apart, disk sometimes nearly impunctate (Fig. 65); female frons beneath transverse swelling almost impunctate (Fig. 2); placoids typically present only on male flagellomeres IV-V, flagellomere III occasionally with small placoid apically (Figs. 61-62); surface of labrum rather abruptly angled down to free margin (Figs. 16, 57-58); apex of female mandible narrowly rounded (Fig. 58). Pronotal pits separate. Mesopleuron usually shiny. Wings weakly to moderately infumate except often clear basally, wings sometimes almost entirely clear in male. Apex of propodeal dorsum sometimes delimited by short transverse carina. Gaster usually black in male, rarely reddish basally; female gaster all red or all black (30% of specimens), occasionally with last two to four segments red. Male sternum VIII usually rounded apically, sometimes truncate or even weakly notched. Female pygidial plate broad (Fig. 68). Males 7-11.5 mm long, females 7-13.5 mm long.

Discussion.—This is the smallest species of *Larra* in the New World, and it is separated from *godmani*, its most similar relative, by the broad female pygidial plate (Fig. 68), and in the male by the presence, in most specimens, of placoids only on flagellomeres IV-V of the antenna (Fig. 61). The abrupt apical declivity of the labrum (Figs. 57-58), and typically polished mesopleuron are additional recognition features, but neither are wholly reliable for separation from *godmani*. In the female the sparse



punctuation of the vertex (Fig. 65) and almost impunctate frons, are distinctive, but some specimens of *godmani* are similar. Occasional males have a small placoid at the apex of flagellomere III (Fig. 62), and of course, a few males of *godmani* have placoids only on IV-V instead of the normal III-V. Association with females may be the only way to identify such males, and even then it is only presumptive. Male sternum VIII is most often rounded in *altamazonica* but in *godmani* is most often notched there.

The occurrence of melanic females in *altamazonica* is apparently higher than in *godmani* with one third of my material having a black gaster or black with the apical segments red. These seem to occur randomly in the western Amazonian Basin. I have two males in which gastral segments I-II are red and the rest are blackish. These are from Trinidad and Guyana, and are the only males of *altamazonica* that I have from these countries. Within the *analis* group this particular color pattern is unique to *altamazonica*.

Distribution (Map 9).—Venezuela, Trinidad, the Guianas, and apparently widely distributed in the Amazonian Basin although most records are from its western fringe. Not known south of the 18th parallel.

Type notes.—Williams' holotype and paratypes have been examined. The type has a red gaster.

ACKNOWLEDGMENTS

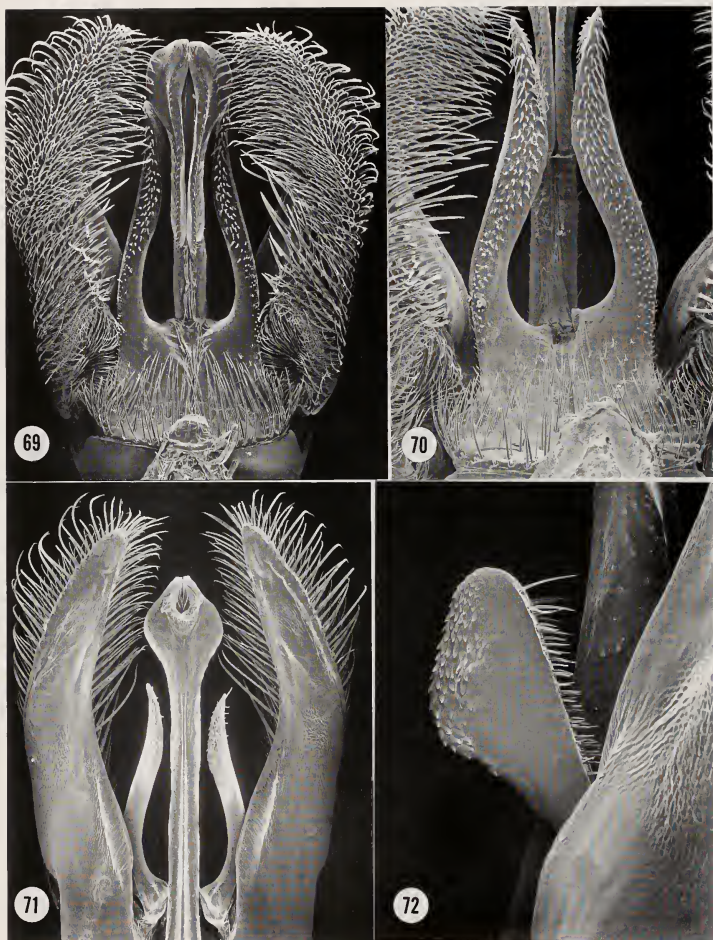
David Wahl, American Entomological Institute, Gainesville, Florida, graciously offered to phylogenetically analyze the species groups of *Larra* and related genera for me; I sent him my data matrix and he ran it in Hennig86. Dave also provided me with the cladogram and consensus tree presented here, and I am especially grateful for his help. Fred Bennett, University of Florida, Gainesville, Florida, sent me copies of rearing records for several generations of *Larra bicolor* and *praedatrix* so that I could identify offspring and correlate males with females. Woj Pulawski, California Academy of Sciences, San Francisco, California offered his insight into various problems that we discussed at length over the telephone. James Carpenter, American Museum of Natural History, New York, and David Wahl critically reviewed the entire manuscript. Eric Grissell, Douglas Ferguson, and Dave Nickle, Systematic Entomology Laboratory, USDA, Washington D.C. reviewed portions of the manuscript; Eric, and other members of the Ashmead Club, graciously put up with my many complaints about how awful *Larra* was as a research problem.



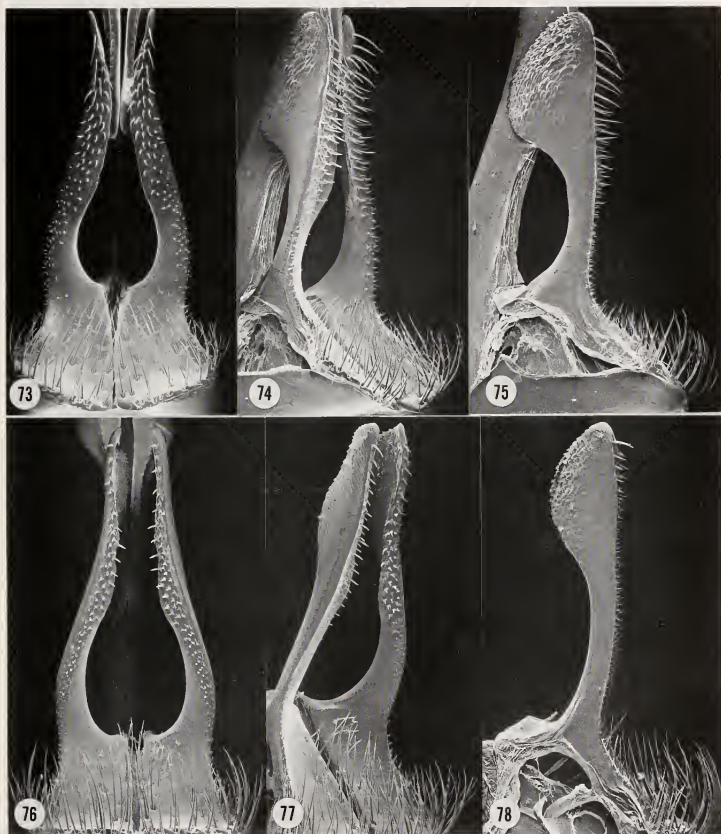


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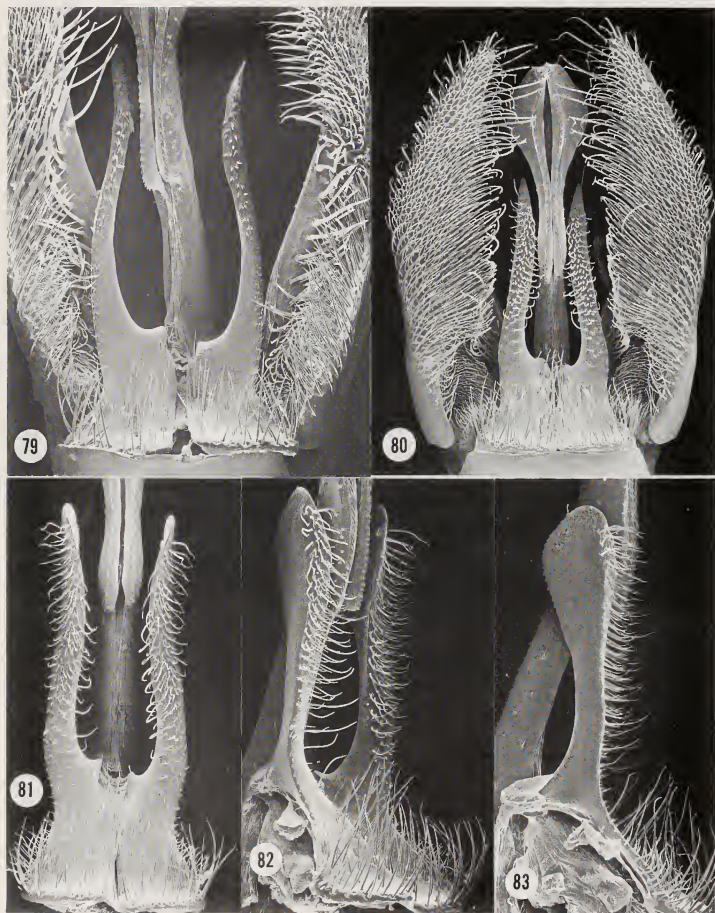
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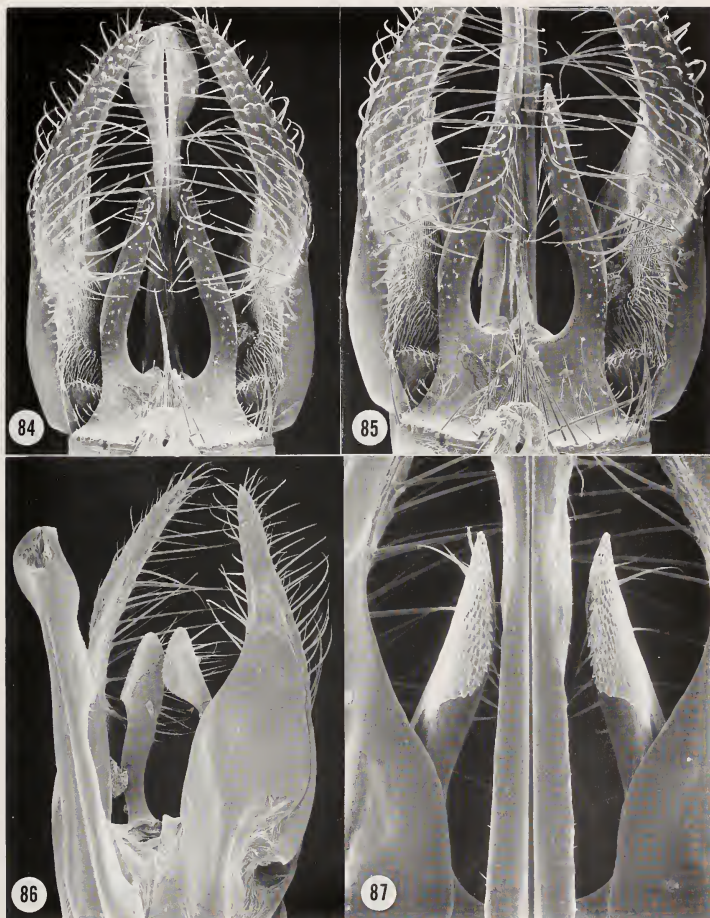
Figs. 69-72. Male genitalia of *bicolor*, specimen from Buena Vista, Bolivia. 69, Ventral view. 70, Ventral view of volsella. 71, Dorsal view. 72, Lateral view of apicodorsal crest of volsellar arm.



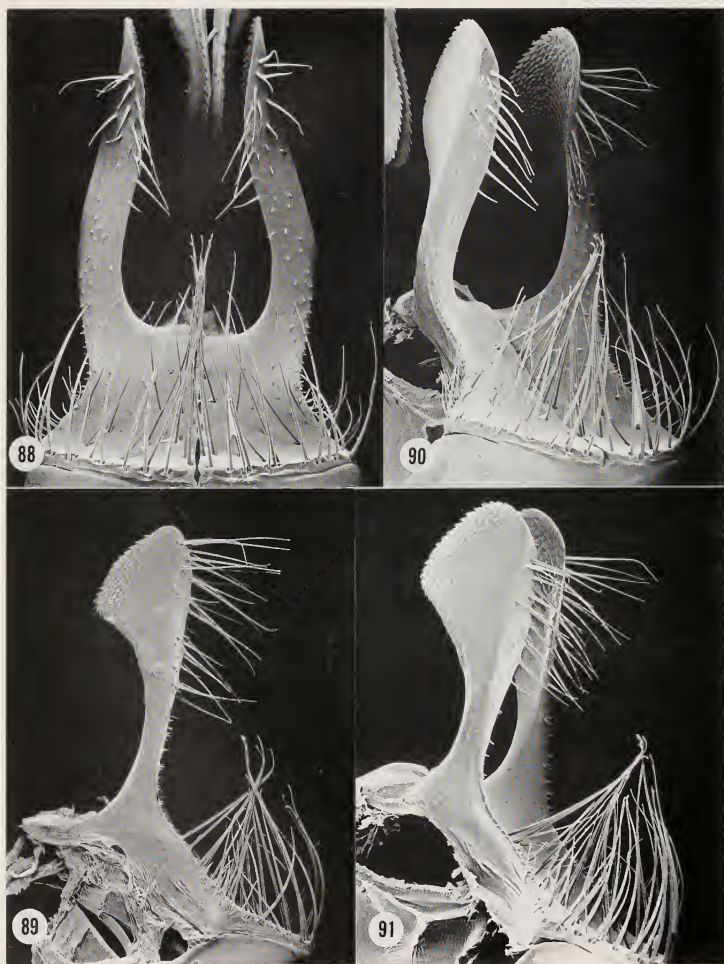
Figs. 73-78. Volsella of male genitalia of *bicolor*. 73-75, Ventral, oblique, and lateral views, respectively of specimen from Saavedra, Bolivia. 76-78, Ventral, oblique and lateral views, respectively of specimen from El Tucuco, Venezuela.



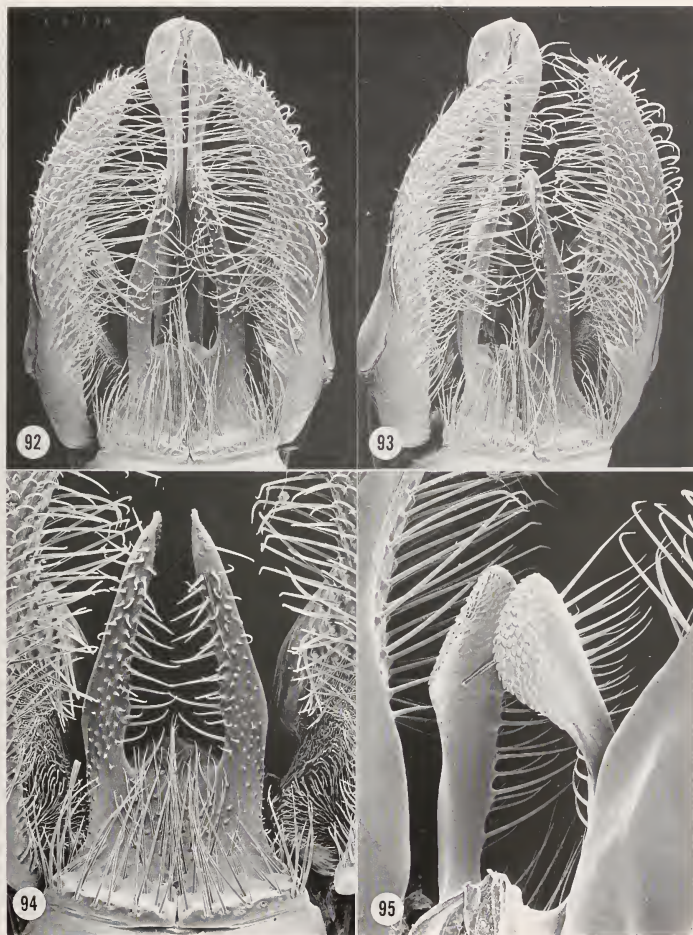
Figs. 79-83. Male genitalia of *bicolor* group. 79, Ventral view of volsella of *bicolor* from Saavedra, Bolivia. 80-83, Venezuelan population of uncertain status in *bicolor* complex. 80, Ventral view of genitalia of specimen from Hato Masaguaral. 81-83, Ventral, oblique and lateral views, respectively, of volsella of specimen from El Limon.



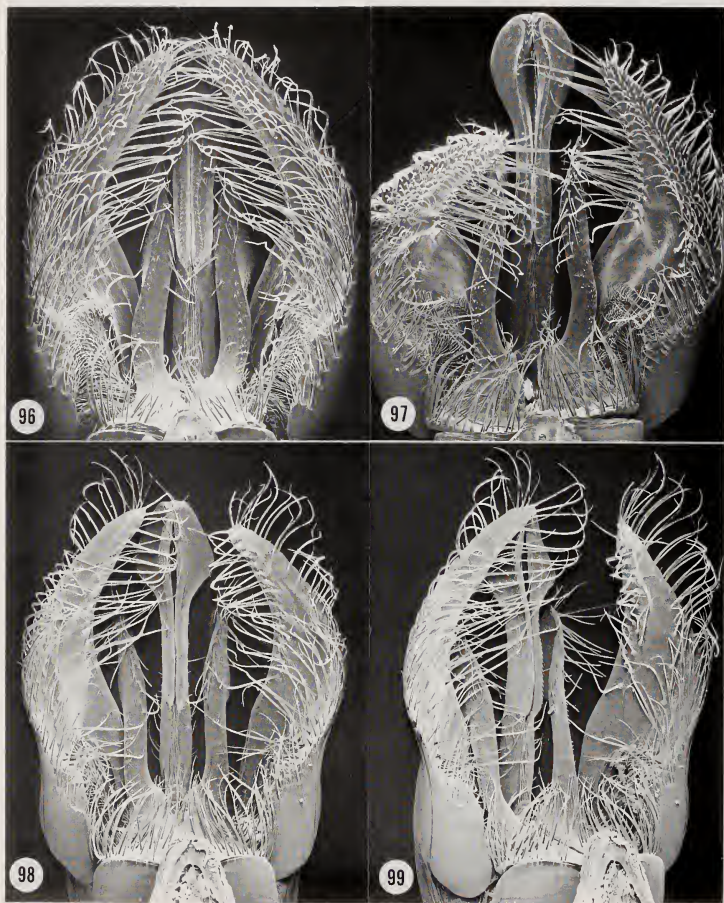
Figs. 84-87. Male genitalia of *praedatrix* from Saavedra, Bolivia (compared and identical with holotype). 84, Ventral view. 85, Ventral view of volsella. 86, Oblique dorsal view. 87, Dorsal view showing apex of volsellar arms.



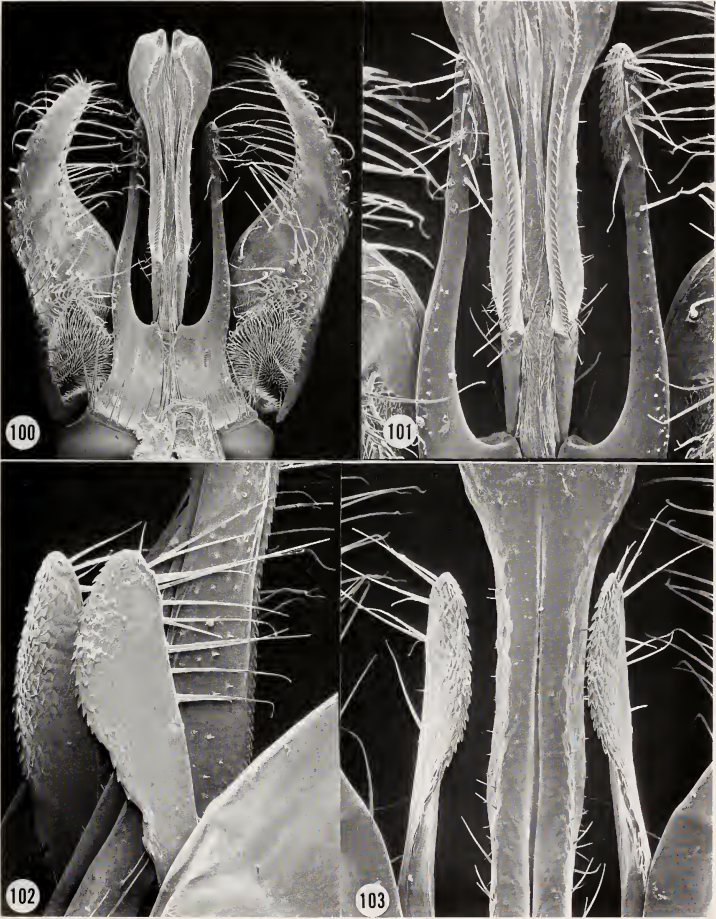
Figs. 88-91. Volsella of male genitalia of *praedatrix* from Saavedra, Bolivia; ventral, lateral and two oblique views, respectively.



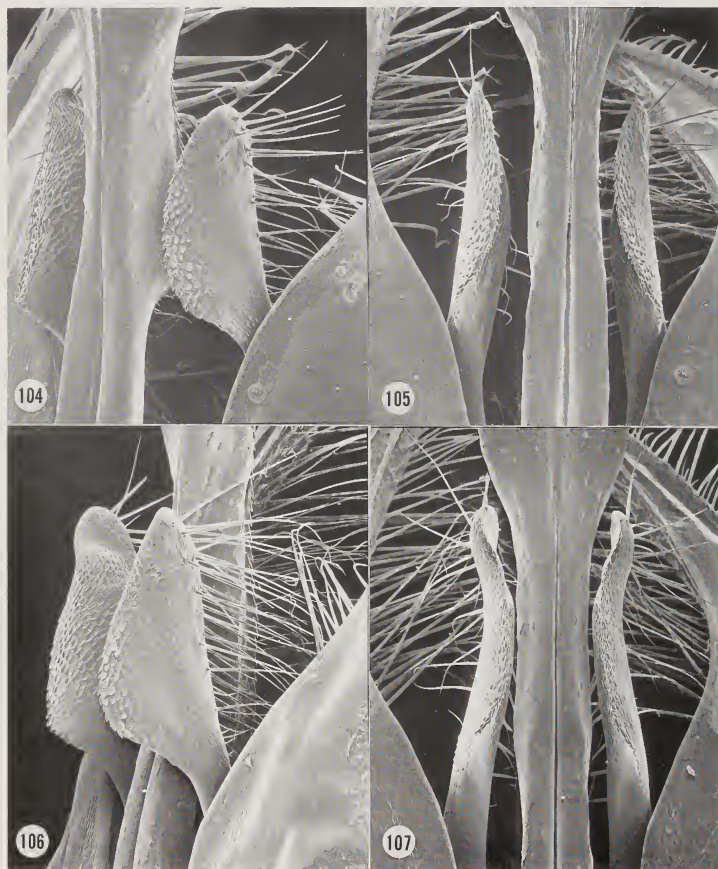
Figs. 92-95. Male genitalia of *praedatrix*. 92-93, Ventral and oblique ventral views, respectively, of specimen from Caaguazu, Paraguay. 94-95, Specimen from Belém, Brasil. 94, Ventral view of volsella showing extension of long apical setae to base of arm along inner margin. 95, Oblique dorsal view of volsellar arms showing long setae to base of arm.



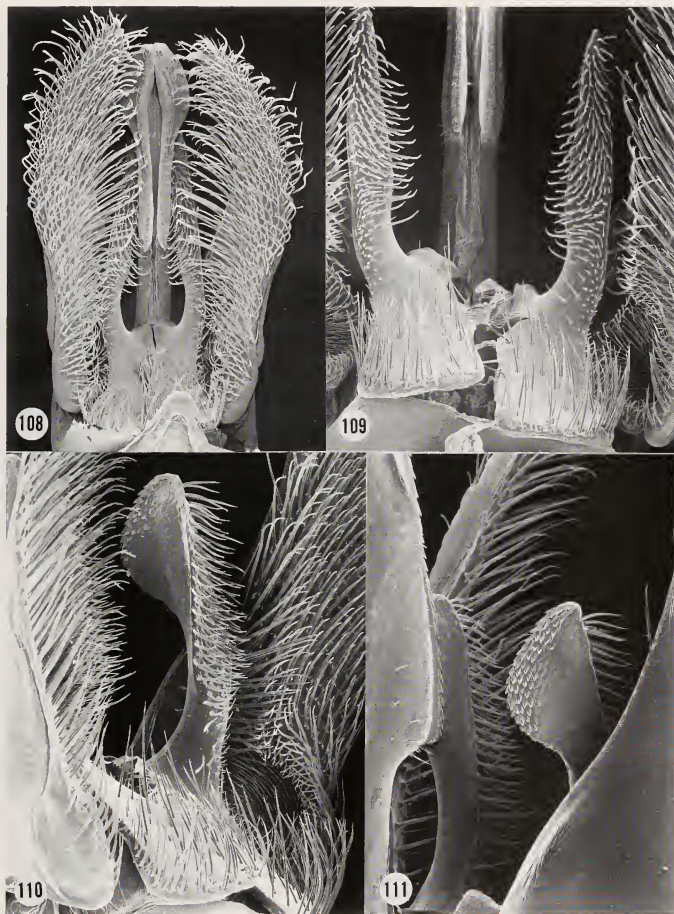
Figs. 96-99. Ventral views of male genitalia of *praedatrix*. 96, Specimen from El Salvador. 97, Specimen from Buenos Aires, Argentina. 98-99, Specimen from Costa Rica.



Figs. 100-103. Male genitalia of specimen of *praedatrix* from San Pedro, Paraguay showing largely asetose gonostyle and straight, narrow volsellar arms. 100, Ventral view. 101, Ventral view of volsella. 102, Oblique dorsal view of apex of volsellar arms. 103, Dorsal view of volsellar arms.



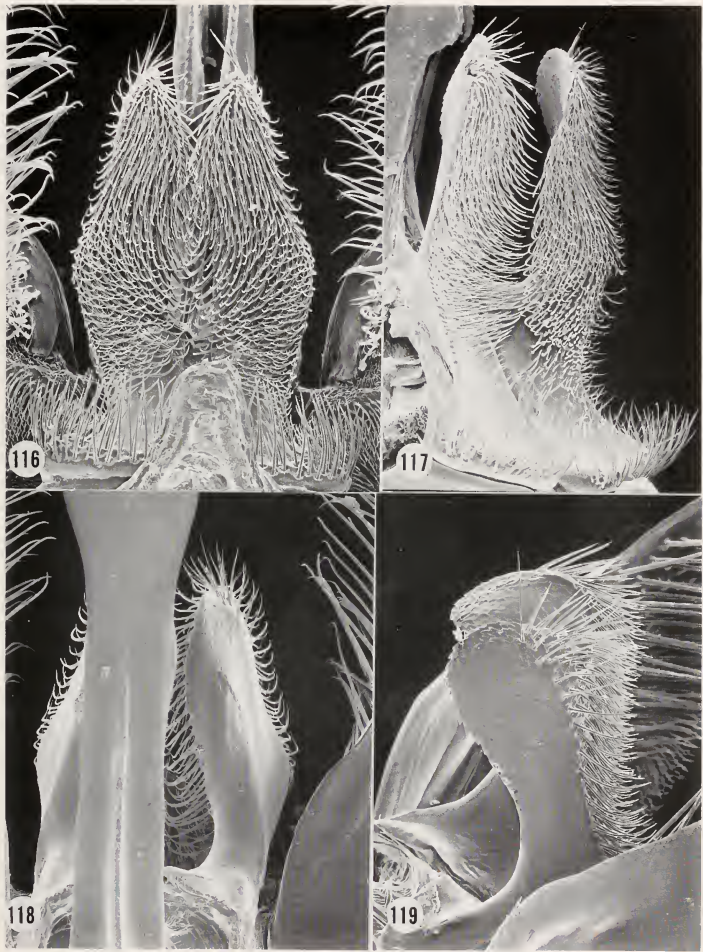
Figs. 104-107. Laterodorsal and dorsal views, respectively, of volsellar apices of *praedatrix*, specimens from Buenos Aires, Argentina. 104-105, Same specimen illustrated by Fig. 97. 106-107, Different specimen.



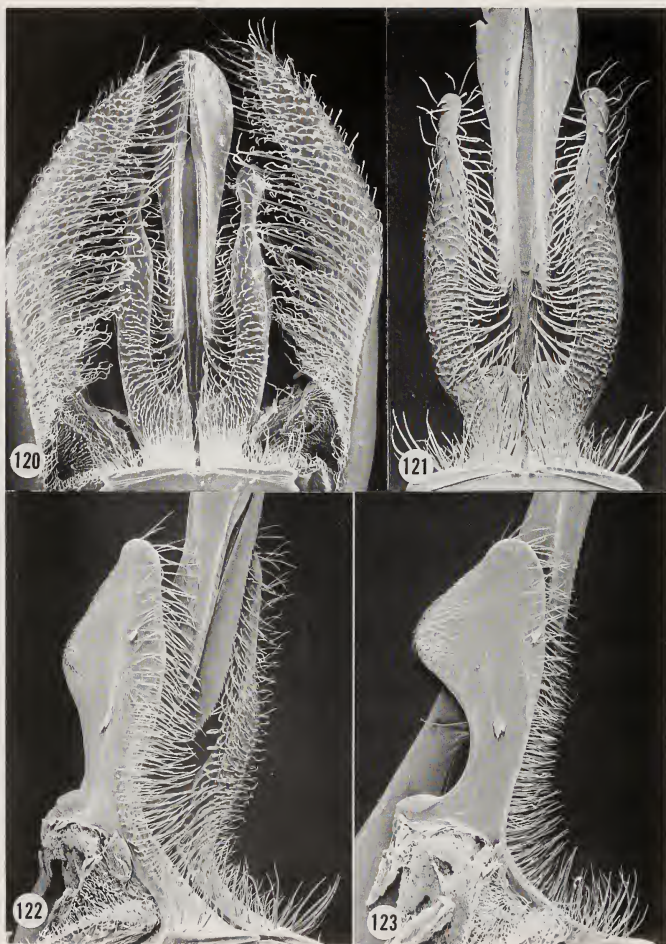
Figs. 108-111. Male genitalia of *stangei*. 108, Ventral view (specimen from Salta, Argentina). 109, Ventral view of volsella of specimen from El Palmar, Bolivia (left and right halves disassociated). 110, Oblique ventral view of volsella of same specimen. 111, Dorsolateral view of apex of volsella of same specimen.



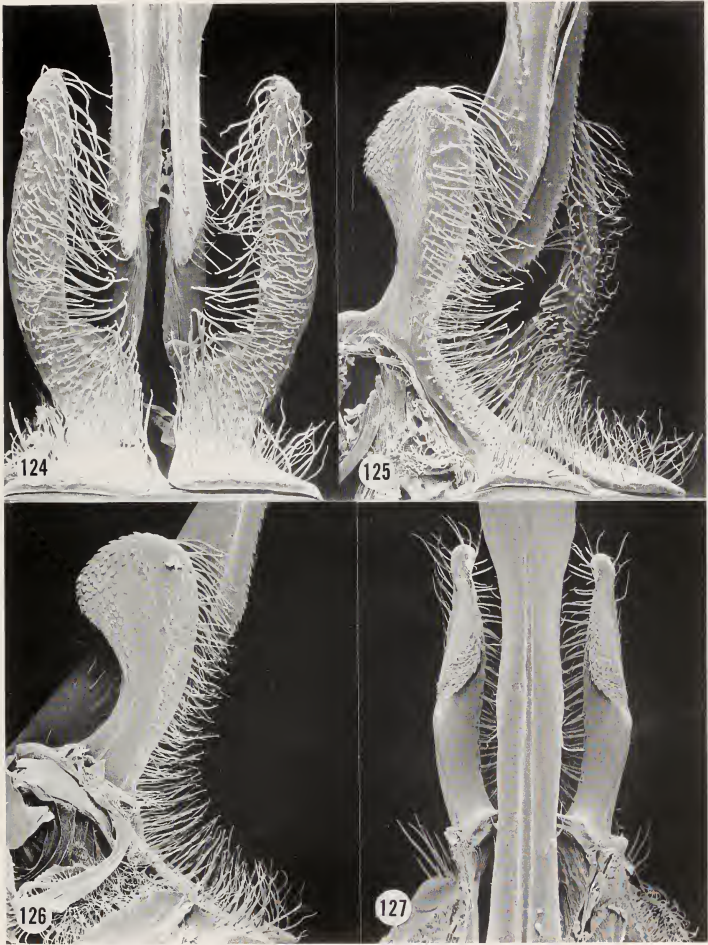
Figs. 112-115. Male genitalia of *princeps*. 112, Ventral view. 113, Lateral view. 114, Dorsal view. 115, Dorsolateral view.



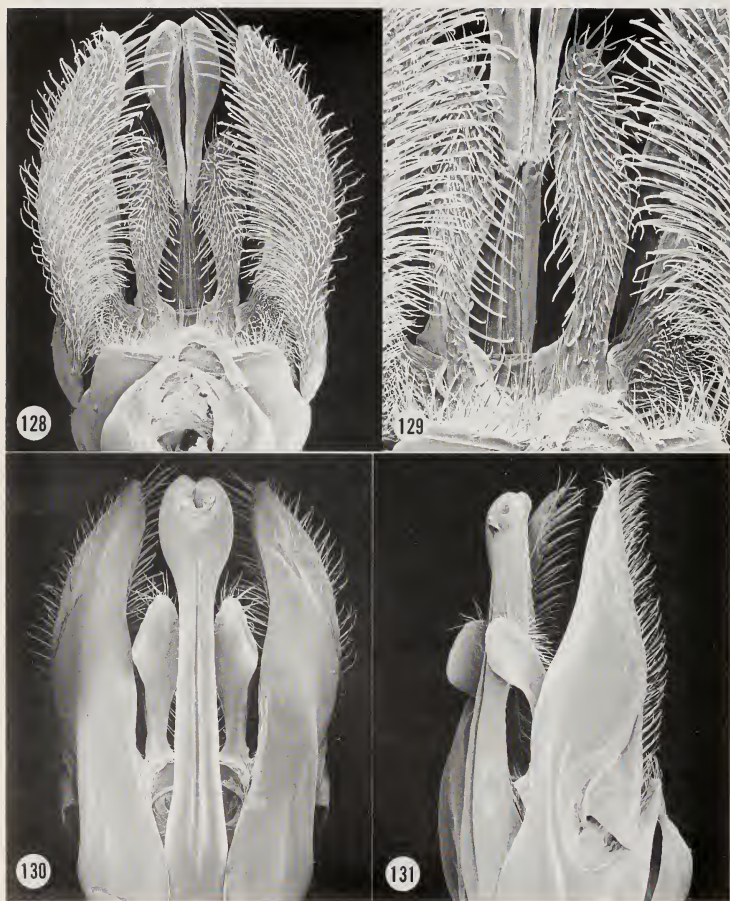
Figs. 116-119. Details of male genitalia of *princeps*. 116, Ventral view of volsella. 117, Oblique ventral view of volsella. 118, Dorsal view of volsellar apex. 119, Lateral view of volsellar apex.



Figs. 120-123. Male genitalia of *burmeisterii* (specimens from Entre Rios, Argentina). 120, Ventral view. 121, Ventral view of volsella. 122, Oblique ventral view of volsella. 123, Lateral view of volsella.



Figs. 124-127. Volsellar details of male genitalia of *burmeisterii* (specimen from Montevideo, Uruguay). 124, Ventral view. 125, Oblique ventral view. 126, Lateral view. 127, Dorsal view.



Figs. 128-131. Male genitalia of *analis*. 128, Ventral view. 129, Ventral view of volsella. 130, Dorsal view. 131, Oblique lateral view.

Nesting Behavior of *Podalonia robusta* (Cresson) (Hymenoptera: Sphecidae)

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Abstract —Twenty-seven females of *Podalonia robusta* were observed nesting in upstate New York during 1980-1985. Females nested solitarily from early June through early October but did not overwinter. They captured cutworms by unearthing them from the soil, stung them several times, cached them, usually on a plant above ground, and dug a burrow some distance away. Prey transport was forward on the ground in a relatively straight line to the nest entrance. Nest closure involved filling the burrow with soil and debris and hammering this fill into place with the head. Nests were unicellular, short, shallow and contained a single prey. Prey consisted of eight genera of hairless, nocturnal-feeding, larval Noctuidae. The wasp's egg was attached to an anterior abdominal segment near the midline. The nesting behavior of *P. robusta* is similar to that of other species in the genus.

The genus *Podalonia* is represented throughout all of the major temperate and tropical regions of the world, except South America (Bohart and Menke 1976). There are 19 species of *Podalonia* in North America north of Mexico (Krombein 1979). O'Brien and Kurczewski (1982) summarized what is known about the biology of the Nearctic and Palearctic species in a paper on the ethology and overwintering of *P. luctuosa* (Smith).

Podalonia robusta (Cresson) is a widely distributed species in North and Central America. It occurs transcontinentally in Canada and the United States as far northward as the North West Territories and the Yukon and as far southward as Costa Rica (Krombein 1979). The species is often confused with *P. violaceipennis* (Lepelletier) because the two are the same size, are black with similar reddish markings and have overlapping geographic distributions, although Murray (1940) gave reliable characters for their separation. In our experience, *P. violaceipennis* tends to be a more coastal species in the northeastern U.S. while *P. robusta* is found more inland, often away from water. The same ecological separation holds true for the two species in Michigan (O'Brien 1989). Our study of the nesting behavior of *P. robusta* was undertaken in order to compare the individual behavioral components of this species with those of other species in the genus, particularly *P. violaceipennis*.

STUDY AREAS

Podalonia robusta was studied at three localities in upstate New York: (1) sandy ridge 2.3 km E Auburn; (2) sandpit 2.0 km S Auburn; and, (3) periphery of active sandpit nr. Junius Ponds, Seneca Falls, all in Cayuga County. Dates of observation are as follows: 27 Aug. 1980, 5 June - 25 Aug. 1981, 30 June - 30 July 1982, 10 Sept. - 3 Oct. 1983, 7 - 23 Sept. 1984, 8 July - 17 Sept. 1985. Voucher specimens of wasps and prey associated with nesting activities are labelled DJP-1, PR81-1-3, PR82-1-6, PR83-1-4, PR84-1-7, PR85-1-6 and have been deposited in the insect museums of Cornell University, The University of Michigan and the S.U.N.Y. College of Environmental Science and Forestry.

FEMALE ACTIVITY

Females of *P. robusta* were observed nesting from 5 June (1981) to 3 October (1983) during partly cloudy to sunny days at ambient temperatures of 18-31°C and soil surface temperatures of 37-46°C from 1100 to 1735 (EDT). The inclusive dates of collection and observation for this species suggests two generations of wasps per year if the average life span of a female is 6-8 weeks, as in the related genus *Ammophila* (Hager and Kurczewski 1986). Adult overwintering is considered unlikely in this species because 11 wasps marked in the fall were

not recaptured the following spring nor were they seen nesting during warm, sunny days in late April and May. During cool weather, in September and October, all observed nest entrances ($N = 13$) faced southward.

HUNTING BEHAVIOR AND PREY CAPTURE

In the genus *Podalonia*, the typical nesting sequence is prey capture, cachement, burrow excavation, prey retrieval, provisioning, and nest closure. Females of *P. robusta* were seen on sand near vegetation, running with their faces close to the ground, abdomens pointed upward and tapping their antennae at the bases of plants. One wasp traversed an area 3 m long in 7 min, turning many circles near vegetation. Her unsuccessful search for prey lasted 44+ min, and then she flew away to feed on *Daucus carota*.

Females that searched for prey tapped their antennae on the ground, buzzed their wings audibly and removed soil with their mandibles and forelegs. Such wasps ($N = 7$) unearthed their prey by digging around the cutworms with the mandibles and forelegs, grasped them with the mandibles and pulled them backwards onto the soil surface. The prey was stung in the ventral side of the body several times, as described for *P. luctuosa* by Steiner (1983). Females then used the mandibles to knead the underside of the anterior segments and midsection of the cutworm's body.

PREY CACHEMENT

Podalonia robusta females ($N = 25$) cached their immobilized prey on low vegetation, especially grass blades or dried stems, from 2 to 6 cm above ground level. One cutworm was placed in the axil of a goldenrod, 22 cm above the ground. Females ($N = 21$) began excavating a burrow within 3 m of the cached prey, but four wasps dug as far away as 5.5, 7, 13 and 16 m from their paralyzed cutworm. The nearest to her prey a wasp dug was 12 cm. Prior to digging, females examined the prey thoroughly with their antennae and mouthparts and nine wasps repositioned, resting and/or remalaxated it.

BURROW CONSTRUCTION

Females of *P. robusta* often made several false starts before staying in one place and excavating a burrow. Wasps began burrows by loosening the soil with the mandibles; they then used the forelegs in unison to throw the soil backward beneath the

raised abdomen. During burrow excavation the wings buzzed audibly. In addition wasps removed soil backward with the psammophore (see O'Brien and Kurczewski 1982) and placed it a few or several centimeters from the opening. Soil deposited near the entrance was subsequently raked backward with the forelegs, forming a fan- or crescent-shaped low mound. Two wasps dug rapidly in comparison to conspecifics and completed burrows in 11 and 13 min, respectively, at soil surface temperatures of 44-46°C. A third female interrupted digging to return to her cached cutworm five times and, upon each return, stung it once in a ventral, anterior segment and then malaxated or fed upon haemolymph exuding from the sting puncture. Following the last sting she rubbed the tip of her abdomen on the sand four times in different areas at distances of 30-150 cm from the quiescent prey. She then cleaned the sting and end of abdomen with the hindlegs, the antennae with the forelegs and resumed burrow excavation. Most wasps groomed themselves upon completion of the burrow.

ORIENTATION

After digging their burrows, females oriented to their nest entrances by walking in circles in either rotation on the ground around them. Some wasps entered and exited from the burrow one or more times while others moved increasingly farther from the entrance, walking in circles. Females then walked or ran toward the cached prey in a rather straight line, sometimes interspersed with short straight flights, but often turned 360° upon landing. Fourteen wasps moved the paralyzed cutworm to a new cache nearer the entrance, returned to the burrow and repeated the orientation behavior described above prior to depositing the prey near the opening. Eleven females proceeded to the nest in a nearly straight line without releasing the prey.

PREY TRANSPORT

Females transported the cutworm, which was often many times heavier than the wasp, to their nests on the ground in an almost straight line. During transport, the prey was held ventral side upward behind the head with the wasp's mandibles and around the thorax with the forelegs. Females, especially those with large cutworms, paused frequently during transport, released the prey and groomed themselves. Some wasps then walked straight forward or in circles, as if attempting to

reorient themselves to their surroundings, before resuming transport to the nest. One wasp released the prey four times and each time stung it in a different abdominal segment, beginning with the second segment and working backward. After her final sting she released the cutworm, reoriented by walking in circles, regripped the prey and walked straight toward the nest entrance. Another wasp continued to recache the prey above ground, walked to the entrance, reoriented, walked back to the cutworm, resumed transport, recached the prey, etc. A third wasp retrieved her paralyzed cutworm and transported it for 16 m on the ground through a dense field in a straight line from the cachement site to the nest entrance. This transport took 13 min, following a 42 min interlude of digging, orientation, reexamination of the prey, etc.

At the nest entrance the cutworm was released with its head toward the opening. The wasp entered the burrow, turned around inside, emerged headfirst, and pulled in the prey headfirst with the mandibles.

One wasp, after taking an exceptionally long (38 mm) cutworm inside, pulled it backwards out of the nest, reentered and began enlarging the burrow. She then emerged headfirst and pulled in the prey.

NEST CLOSURE

After ovipositing on the cutworm, females appeared headfirst in their entrances ca. 1 min after entry, began breaking off pieces of the entrance with the mandibles and placed these inside the burrow. Wasps then either threw soil backward into the opening with the forelegs or retrieved clumps of soil from the surface with the mandibles and placed these inside. This soil was packed into the opening with the head. Some wasps then brought pebbles, seeds, dried leaves, twigs, and/or agglutinated sand clumps from a bee tumulus and incorporated these into the fill. A few females continued to place pebbles up to 9 mm in diameter, twigs, seeds and other debris atop the filled entrance. Alternately, they threw loosened sand onto the fill and surrounding area with the forelegs which totally concealed the entrance. Nevertheless, a few filled nests remained depressed 2 mm at the entrance. Upon completion, wasps hovered in flight for a second or two and then flew away. One closure, completed at 1432 took 11 min. Excavation of another nest revealed that a female had stayed inside of her cell, head outward, atop the cutworm for 21 min without ovipositing, possibly in response to a cleptoparasitic fly attack.

NEST

Nests of *P. robusta* were simple unicellular burrows which sloped downward and were either straight, C- or L-shaped. The circular entrances were 5-9 (mean = 6.9, N = 16) mm and the burrows 5-9 (mean = 6.8, N = 20) mm in diameter. The burrows had a mean length of 24.5 (range = 10-38, N = 25) mm and a mean cell depth of 20.7 (range = 10-38, N = 25) mm. Cells ranged in length from 15-25 (mean = 19.4, N = 25) mm and in width from 7.5-17 (mean = 10.7, N = 25) mm. Tumuli associated with some of these nests measured 35-45 (mean = 40.1, N = 7) mm long, 25-45 (mean = 36.0, N = 7) mm wide and 13 mm (N = 1) high. Differences in nest dimensions between spring and midsummer nesting aggregations of wasps were insignificant (t test, $P > 0.05$).

PREY

Podalonia robusta females preyed upon soil-dwelling, larval Noctuidae. A single paralyzed cutworm was placed in each cell. Prey were determined as follows: *Aletia oxygale* (Grote) (1), *Apamea* sp. (2), *Caenurgina erechtea* Grote (1), *Eupsilia devia* (Grote) (2), *Euxoa* sp. (2), *Lacanobia subjuncta* (Grote & Robinson) (2), *Protorthodes oviduca* (Guenée) (3), ? *Protorthodes* sp. (1) and *Pseudorthodes vecors* (Guenée) (1). Cutworm prey ranged in wet weight from 166 to 698 (mean = 330.1, N = 24) mg and the female wasps weighed 56-83 (mean = 73.8, N = 6) mg. The mean weight of prey to wasp ratio was 4.5: 1.

EGG

Each egg of *P. robusta* was attached by its anterior end to the abdominal midline of the prey; the posterior end of the egg extended away from the midline of the prey's body (N = 17). Live eggs ranged from 3.0 to 4.0 (mean = 3.6, N = 3) mm long and from 0.8 to 0.9 (mean = 0.9, N = 3) mm wide. They were placed on the left (6) or right (11) sides of the cutworm and were affixed to the first (1), second (2), third (5), fourth (8) or fifth (1) abdominal segments.

CLEPTOPARASITISM

Females of *P. robusta* were trailed and their prey or entrances larviposited on/within by three species of Miltogrammini: *Senotainia trilineata* (Vander Wulp), *S. vigilans* Allen and *Sphenometopa tergata* Meigen (Spofford and Kurczewski 1990). One cutworm attacked during prey transport contained 12

maggots of *S. vigilans*. Two wasps attracted three *S. vigilans* while fighting with each other. The first female went off hunting trailed by one fly and the second left hunting trailed by the two other flies. Another *S. vigilans* followed a wasp during prey transport and attempted twice to larviposit on the cutworm. After the *P. robusta* cached her prey, the fly perched motionless on a plant nearby. As the wasp walked away, searching for a place to dig a burrow, the fly followed her and ignored the cached cutworm. One wasp, whose prey was larviposited upon by an *S. trilineata* during transport, did not exit from her nest after placing the cutworm inside. During excavation of the nest, several minutes later, she was observed resting atop the prey which was in a curled, C-position in the cell. There was no wasp's egg on the cutworm. We believe that the wasp was in the process of cleaning maggots from the prey when we unearthed her, but prey cleaning has not been substantiated for species in this genus.

DISCUSSION

In many genera of Sphecidae, certain behavioral characteristics apply to all or most congeners, and species of *Podalonia* are no exception. Key differences exist between species of *Podalonia* as to: (1) whether adult females overwinter; (2) whether the wasps construct burrows before or after capturing prey; and, (3) kinds of prey. Murray (1940), based upon Newcomer's (1930) and Hicks' (1931) observations and his own collecting records, concluded that some adult females of *P. communis* and *P. luctuosa* overwinter. Females of several European species of *Podalonia* are also believed to overwinter (Roth 1928, Maneval 1939, Grandi 1961). O'Brien and Kurczewski (1982) marked *P. luctuosa* females with paint in late summer and recaptured some of them the following spring to confirm overwintering in this species. According to the present study, adult females of *P. robusta* do not overwinter.

At least two species of Nearctic *Podalonia*, *valida* (Steiner 1975) and, sometimes, *occidentalis* (Evans 1987) dig their burrows before they hunt for prey. This behavior has also been reported in two exotic species of the genus (Tsuneki 1968, Bohart and Menke 1976). The advantages and disadvantages of digging the burrow before prey capture have been reviewed by Evans and West-Eberhard (1970) and Iwata (1976). *P. robusta* invariably dug its burrow after capturing prey, in our observations of 27 wasps.

The majority of species of *Podalonia* prey upon hairless, nocturnal-feeding, noctuid larvae (Bohart and Menke 1976, Krombein 1979). *P. valida*, in contrast, hunts diurnal "wooly bears" of the genus *Estigmene* (Arctiidae) (Steiner 1974), and *P. occidentalis* is a specialist on tent caterpillars of the genus *Malacosoma* (Lasiocampidae) (Evans 1987). Williams (1928) noted that *P. violaceipennis* also captured tent caterpillars in California, but it is likely that he, too, was observing *P. occidentalis* (Evans 1987). Balduf (1936) reported that *P. violaceipennis* hunts mature larvae of the notodontid *Symmerita albifrons* S. & A., but his report may have involved misidentification of the wasp. Roth (1928) observed *P. hirsuta* Scopoli preying upon gypsy moth larvae (Lymantriidae) in Europe. That three species of *Podalonia* capture hairy, arboreal, lepidopterous larvae and numerous other species prey upon hairless, nocturnal-feeding cutworms is a difference that provides the basis for further study of prey selection in the genus.

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Biological and Taxonomic Studies of *Chartocerus subaeneus* (Hymenoptera: Signiphoridae), a Hyperparasite of Mealybugs

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Abstract.— *Chartocerus subaeneus* (Foerster), an obligatory direct hyperparasite of mealybugs, is redescribed and its developmental stages are described and illustrated. A lectotype is designated. This deuterotokous species develops ectoparasitically on fully developed larvae and pupae of various primary encyrtid parasites in mummified mealybugs. When reared on *Tetracnemoidea peregrina* (Compere) in the long-tailed mealybug, *Pseudococcus longispinus* (Targioni Tozzetti) at 28°C, females lived for 25 days and oviposited throughout their lifetime. Fecundity was high, averaging 163 eggs per female or 6.8 eggs per day. Adult females host-fed regularly, and this prolonged their life span considerably. They were susceptible to low relative humidity. Development from egg to adult emergence took 16.4 days. The developmental threshold was 14.8°C, and the thermal constant was 221.5 days-degrees.

The biology of hyperparasitic Hymenoptera has been relatively little studied (see Rosen 1981, Sullivan 1987 and Viggiani 1990 for recent reviews). Of the Signiphoridae known as hyperparasites, only two species have been studied in any detail: *Chartocerus elongatus* (Girault) by Clausen (1924) and *Signiphora coquillettii* Ashmead by Woolley and Vet (1981). Somewhat more information is available on the biology of Signiphoridae acting as primary parasites, all of which are species of *Signiphora* that attack armored scale insects. Quezada et al. (1973) provide the most complete biological information for any signiphorid in their study of *Signiphora borinquensis* Quezada, DeBach and Rosen, DeBach et al. (1958) and Agekyan (1968) provide details for *Signiphora merceti* Malenotti, and Woolley (1988, 1990) reviews the remaining available information.

A little-known hyperparasitic signiphorid, *Chartocerus subaeneus* (Foerster), was found to overwhelm mass cultures of *Tetracnemoidea peregrina* (Compere) (Hymenoptera: Encyrtidae) during a highly successful campaign for biological control of the long-tailed mealybug, *Pseudococcus longispinus* (Targioni Tozzetti) (Homoptera: Pseudococcidae), which was the cornerstone of an effective integrated pest management program on avocado in Israel (Swirski et al. 1980, Swirski and Wysoki 1988). In field samples, on the other hand, this hyperparasite was quite rare. A study of its taxonomy and biology was undertaken in order to

contribute to our knowledge of hyperparasites and signiphorids.

MATERIALS AND METHODS

Chartocerus subaeneus was originally obtained from a laboratory mass culture at the Volcani Center, Bet Dagan, Israel. Cultures of the hyperparasite were maintained at 28±1°C and >50% RH, in ventilated plastic cages, 15 x 25 x 35 cm or so, with *Tetracnemoidea peregrina* serving as primary host and the long-tailed mealybug, *Pseudococcus longispinus*, infesting sprouting potatoes, as secondary host. Both the primary and secondary (mealybug) hosts were reared at the Volcani Center on sprouting potatoes, at 26±2°C and >65%.

Material for description of adults and developmental stages was obtained from the laboratory cultures. In biological experiments, parasitized mealybug mummies were glued to small cards (2.5 x 3 cm) with neutral glue (Sachinata Mucilage Glue, Japan) and presented to newly-emerged wasps in small plastic cups. Unless stated otherwise, all experiments were held at 28±1°C and >50% RH, and the wasps were provided with honey streaks for food.

TAXONOMY

The genera of Signiphoridae have recently been reviewed by Woolley (1988), who provides a key to

genera and species groups, diagnostic characteristics, discussions of various anatomical characters, and hypotheses for phylogenetic relationships. Rozanov (1965) treated *Chartocerus* as containing three subgenera, and referred *C. subaeneus* to the subgenus *Signiphorina*. Woolley (1988) provided evidence for monophyly of *Chartocerus* and the nominate subgenus, but was unable to find evidence for monophyly of the other two subgenera. *Chartocerus* is in need of revision on a worldwide basis, and consequently most species are difficult to identify. *Chartocerus subaeneus* is most closely related to *elongatus* (Girault), *novitzkyi* Domenichini, *fimbriae* Hayat, and *intermedius* Hayat. Novitzky (1954) redescribed and figured *subaeneus*, Domenichini (1955) compared *subaeneus* with *elongatus* and *novitzkyi*, and Hayat (1970, 1976) compared *subaeneus* with *fimbriae* and *intermedius*. We have determined the identity of our material based on examination of Foerster's types, the literature, and comparison with specimens determined by Sugonyaev and Ferrière. In addition to Israel, *Chartocerus subaeneus* is reported from Western Europe, the European part of the U.S.S.R., Turkey and Soviet Central Asia.

In view of the inadequate state of the systematics of this group, a detailed redescription is presented for future reference.

ADULT MORPHOLOGY

Terminology for anatomical structures follows Woolley (1988). In particular, mesosoma refers to thorax plus propodeum, metasoma refers to the abdomen posterior to the propodeum, and numbering of terga and sterna (e.g., T2, S2) refers to metasomal terga and sterna. The apparent ninth tergum in females is called the epiproct for reasons discussed by Woolley (1988).

Chartocerus subaeneus (Foerster)

Platostichus subaenea Foerster 1878, Verh. Nat. Ver. Preuss. Rheinh. 35: 69.

Thysanus subaenea: Dalla Torre 1898, Catalogus Hymenopterorum, Lipsiae 5: 223.

Signiphorina mala Nikol'skaya 1950, Dokl. Akad. Nauk SSSR 75: 19-21.

Signiphorina subaenea: Novitzky 1954, Ann. Fac. Agr. (N.S.) 2: 245-255.

Signiphora (*Signiphorina*) *subaenea*: Peck et al. 1964, Mem. Entomol. Soc. Can. 34: 90-91.

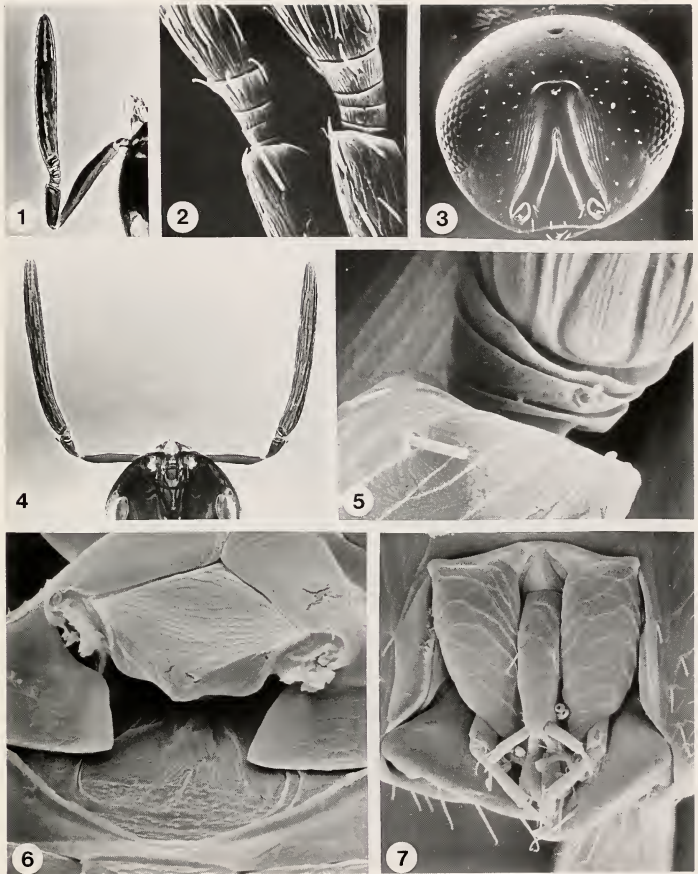
Chartocerus (*Signiphorina*) *subaeneus*: Rosanov 1965, Entomol. Obozr. 44: 878.

Diagnosis.—Inasmuch as *Chartocerus* is in need of comprehensive revision, it is no doubt premature to attempt to distinguish *subaeneus* from all species with which it might be confused. It appears to be most similar to *C. elongatus*, *C. novitzkyi*, *C. fimbriae* and *C. intermedius*. In *subaeneus*, the medial denticles of the male genitalia are robust, curved and long, extending approximately half the length of the digiti, and they are inserted on a strongly sclerotized region between the bases of the digiti (Fig. 26). The medial denticles in *elongatus* are less robust, straight, and shorter (about 1/3 the length of the digiti), and they are not inserted on a sclerotized region (cf. Fig. 4.8, Domenichini 1955). In *novitzkyi*, the medial denticles are long and straight, almost the length of a digitus, and a sclerotized region is not apparent at their bases (cf. Fig. 4.9, Domenichini 1955). According to Hayat (1970, 1976), *fimbriae* and *intermedius* can be distinguished from *subaeneus* by the longer marginal fringe on both fore and hind wings, and the yellow middle tibiae of all legs (middle and hind tibiae are black in proximal half in *subaeneus*).

Female.—General coloration shining black; antennae dark brown; eyes and ocelli black; all tarsi yellowish, fore tibiae pale, middle and hind tibiae black in proximal half and pale distally, other segments of all legs black. Fore wing with alternating, broad hyaline and dark bands (Fig. 13). Hind wing hyaline.

Length 0.95-1.15 mm. Head (Figs. 3, 8) with frontovertex broad, wider than long, transversely striate, bearing sparse short setae. Cheek length not exceeding 2/3 length of eye. Face longitudinally striate, bearing sparse short setae. Eyes with sparse, short inter-ommatidial setae. Ocelli in an obtuse triangle; the posterior pair at about their own diameter from inner orbits. Antennal toruli (Fig. 3) about their own diameter from oral margin; scrobes convergent, the area between them not elevated.

Mandibles bearing long setae, the two denticles subequal in length, the dorsal one somewhat truncate. Maxillary palpi (Fig. 7) 2-segmented, apical segment the longest, bearing an apical spine; labial palpi 1-segmented, bearing an apical spine and a subapical seta. Antenna (Figs. 1, 2) 7-segmented (1141), all but the first 3 funicular segments bearing short setae. Radicle bearing a few sensory setae at base. Scape 4.8 - 6.5 times as long as wide. Pedicel 2.0 - 2.75 times as long as wide, usually 1.5 - 2.0 times as long as funicle. First funicular seg-



Figs. 1-7. *Chartocerus subaeneus*. 1, Female antenna 2, Female antennae: pedicel, funicle and base of club (SEM). 3, Head, frontal view; antennae removed to show toruli and scrobes (SEM). 4, Male head and antennae. 5, Male antennal funicle (SEM). 6, Female prosternum, ventral pronotum, prepectus, and mesepisternum in ventral view; fore coxae removed (SEM). 7, Female mouthparts, ventral aspect, showing maxillae and labium (SEM).

ment minute, 6-7 times as wide as long; second and third segments subequal in length, twice as long as the first, 2-4 times as wide as long; fourth segment about 1/3 as long as the third, 1.7-3.0 times as wide as long. Club 5.0-9.3 times as long as wide, 1.5-1.6 times as long as scape and about 6 times as long as funicle, bearing 4-6 longitudinal sensilla, 0.26-0.32 length of club, and several fingerlike sensilla at tip.

Mesosoma (Figs. 8-10) transversely imbricate, bearing sparse short setae. Pronotum usually 2/5 length of mesoscutum in dorsal view, bearing a transverse row of short setae along posterior margin. Mesoscutum 2.3-3.0 times as long as scutellum, bearing 6-19 setae, those in postero-lateral corners larger. Scutellum bearing a row of 7-12 short setae along posterior margin, with a pair of submedian discoid sensilla. A pair of lateral internal costulae on scutellum, visible only in cleared slide mounts (compare Figs. 8 and 9), set off the triangular apparent axillae, each of which bears a single large seta. Metanotum with medial portion faintly striate and devoid of setae; lateral lobes smooth except for some reticulation near margins, each bearing a pair of minute setae. Propodeum (Figs. 9, 10) length 0.6-0.8 greatest width, 0.55-0.72 length of mesoscutum, 1.66-1.75 times as long as scutellum, 2.5-3.5 times as long as metanotum; smooth laterally, rather faintly reticulate mesad of spiracles, with medial sclerite triangular and strongly reticulate, apex not quite reaching posterior propodeal margin. Prepectus fused with ventral mesepisternum; the membrane between it and the prosternum, underneath the fore coxae, bearing numerous papillae (Fig. 6).

Metasoma (Figs. 9, 12) subequal in length to the head and mesosoma combined. First tergum (= second abdominal) (Figs. 9, 10) short, smooth, weakly bilobed, not overlapped by propodeum; T2-T6 reticulate, bearing 4-9 setae on each side, with a discoid sensillum anterad of each setiferous area; T2 the longest; T7 (Fig. 25) bearing a transverse row of 8 setae, with a pair of submedian discoid sensilla between the spiracles; T8 (Fig. 25) represented by a narrow transverse plate and two lateral lobes bearing the cerci, each with two long setae and one short seta; epiproct rhomboid. Sixth sternum almost at apex of metasoma and distinctly bilobed medially. Second phragma (Fig. 12) 1.53-1.87 times as long as wide, reaching well beyond base of ovipositor to level of fifth tergum. Ovipositor nearly twice as long as middle tibia (1.80-1.98); ovipositor sheaths longitudinally striate.

Tarsi of all legs pentamerous (see Fig. 12); strigil (Fig. 15) well developed; middle femur (Fig. 16) bearing 2 or 3 long spines postero-apically, one short apical spine, and a row of short setae dorsally; middle tibia bearing 2 long setae and 2 shorter setae dorsally, in addition to numerous short setae; mid-tibial spur (Figs. 16, 17) 4/5 length of corresponding basitarsus or more (0.78-0.93), bearing a row of 4-5 teeth.

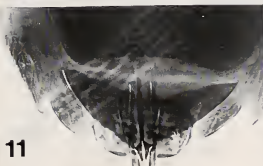
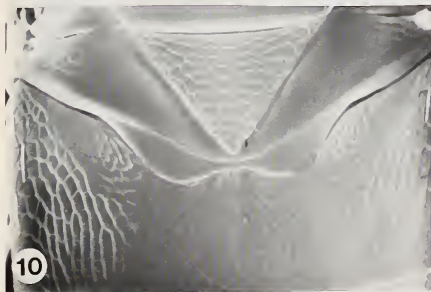
Fore wing (Fig. 13) about 3 times as long as wide (2.8-3.1); longest marginal cilia 1/2-2/3 width of disk. Submarginal vein 3/4 to nearly as long as marginal vein, bearing 2 setae and 13 bullae; marginal vein bearing 4 long setae along anterior margin and 4-5 short ventral setae; stigmal vein about 1/5 length of marginal vein, bearing a single seta and 3 discoid sensilla. Costal cell bearing a single dorsal seta; disk otherwise bare except for 5-7 minute ventral setae below junction of submarginal and marginal veins. An oblique fold near center of disk, beginning below apex of venation.

Hind wing (Fig. 14) about 5 times as long as wide (4.1-5.5); longest marginal cilia 3/4 width of disk or more (0.75-0.93); disk bare except for one short seta below apex of marginal vein. Marginal vein bearing one long proximal seta followed by 2-5 shorter setae, 2 hamuli and 3 straight spines at apex.

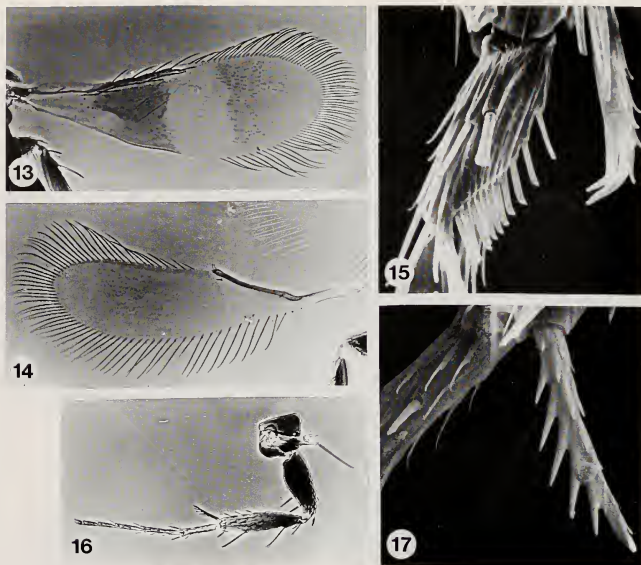
Male.—Similar to female in structure, chaetotaxis, sculpture and coloration, differing mainly in antennal and genital characters.

Antenna (Fig. 4) six-segmented (1131). Scape as in female; pedicel more pyriform, 2.0-2.5 times as long as funicle; funicular segments (Fig. 5) ring-like, subequal in width, the first 4 times as wide as long, the second 3 times as wide as long and twice as long as the first, the third twice as wide as long and twice as long as the second; club longer than in female, 11-14 times as long as wide, 15 times as long as funicle, bearing about 20 longitudinal sensilla.

Mesoscutum and scutellum each bearing 7-9 setae. Eighth sternum (Fig. 26) broadly crescent-shaped and rounded posteriorly, 3 times as wide as long at midline, about 1.2 times as wide as seventh sternum. Genitalia (Fig. 26) 1/2-2/3 length of middle tibia, ventral surface of phallobase with distinct longitudinal thickening at midline, running from between bases of digiti almost to apex, digitus with apical denticle about 1/3 its length, medial denticles slightly curved and 1/3-1/2 length of digitus (excluding apical denticle), phallobase sclerotized at base of medial denticles



Figs. 8-12. *Chartocerus subaeneus*. 8, Female head, pronotum, mesoscutum and scutellum (SEM). 9, Female mesosoma and base of metasoma. 10, Female propodeum and base of metasoma (SEM). 11, Male, apex of metasoma and genitalia, ventral aspect. 12, Female mesosoma and metasoma, showing second phragma and ovipositor.



Figs. 13-17. *Chartocerus subaeneus*, female: 13, Fore wing. 14, Hind wing. 15, Calcar and strigil on fore leg (SEM). 16, Middle leg. 17, Mid-tibial spur (SEM).

and bearing a pair of lateral setae, slightly longer than medial denticles. Our material agrees well with the Fig. of Domenichini (1955), but the medial and apical denticles are somewhat longer relative to the digiti in our specimens.

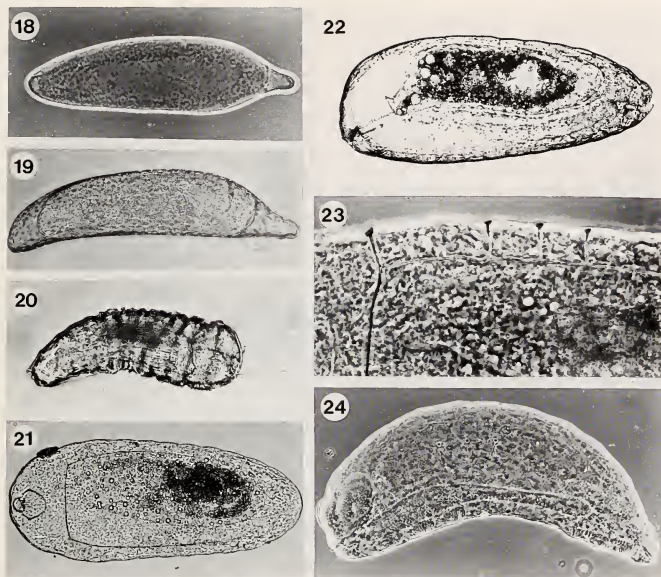
Material examined.—Redescribed from 20 females and 13 males, reared in laboratory culture on *Tetraneimoidea peregrina* in the long-tailed mealybug, *Pseudococcus longispinus*, on potato sprouts, Rehovot, Israel.

Types.—Lectotype male (present designation). "17/610, Frst, *Plastocharis subaeneus* Frt., Zool. Mus. Berlin." Mounted on a pinned card between small pieces of glass cemented across an opening. The mountant has partially dried out and the specimen is crushed and flattened but otherwise in reasonably good condition. One fore wing and the head are dissected and only the antennal scapes and a single club remain. This specimen is here

designated lectotype and has been labelled accordingly. It is in the Museum für Naturkunde der Humboldt Universität zu Berlin. Paralectotype. "17/584, Aachen, Frst, *Plastocharis subaeneus* Frst, Zool. Mus. Berlin." Mounted in a manner similar to the lectotype but the mountant is more badly dried out. Foerster (1878) stated that this species was described from male and female material; however, as Novitzky (1954) pointed out, this specimen is a male *Thysanus*, probably *ater* Haliday. Also housed in the Museum für Naturkunde.

DEVELOPMENTAL STAGES

Mummies of the long-tailed mealybug containing advanced larvae or pupae of *T. peregrina* were exposed to females of *C. subaeneus* for 24 hours, and were then kept at 32°C. At daily intervals, 30 mummies were dissected in saline solution under



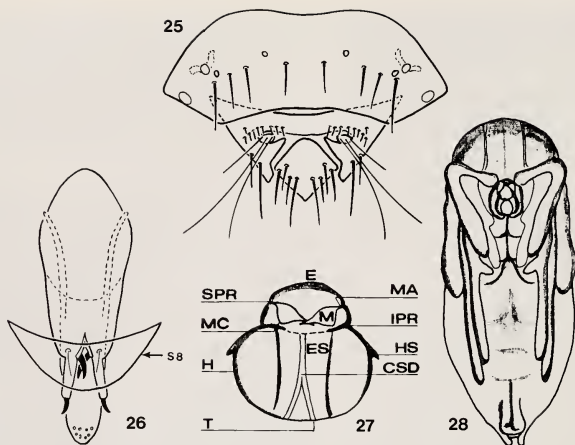
Figs. 18-24. *Chartocerus subaeneus*, developmental stages. 18, Egg, several hours after oviposition. 19, Egg, one day after oviposition. 20, First instar larva. 21, Second instar larva, showing the cephalic skeleton and respiratory system. 22, Second instar larva, showing the oesophagus, midgut and salivary gland. 23, Second instar larva: spiracles. 24, Third instar larva.

a stereoscopic microscope. Eggs and first-instar larvae were mounted directly in Hoyer's medium. Later developmental stages were soaked in chlorophenol solution for 2-7 days prior to mounting in Hoyer's medium. For observation of respiratory systems, live larvae were immersed in bromophenol solution on a slide, covered with a cover slip and studied immediately under a phase-contrast microscope.

The egg (Figs. 18, 19) is hymenopteriform, banana-shaped, with an elongate projection (or short stalk), grayish white, 265-300 μ long, and 75-110 μ wide. During the first few hours its contents appear as a mottled mass surrounded by a membrane, then the mouthparts and midgut become visible.

The larva (Figs. 20-24) develops through 4 instars. These are distinguishable by their general dimensions and by the shape and size of their

mandibles. All instars are hymenopteriform, with the head and 13 body segments evident, and all have 4 pairs of spiracles - in the mesothorax and first 3 abdominal segments (Fig. 23). First instar larva (Fig. 20) transparent white, elongate, tapering posteriorly, 215-260 μ long and 60-75 μ wide; mandibular denticle somewhat curved, 4 μ long. Second instar (Figs. 21-23) of typical chalcidoid form, with the head partially withdrawn into the thorax, 325-480 μ long and 125-200 μ wide; mandibles beak-like, 6 μ long, with a broader base than in the first instar. The oesophagus, midgut and salivary gland are clearly evident at this stage (Fig. 22), as are the cephalic skeleton and respiratory system (Figs. 21, 23). The latter, as in the first instar, consists of two lateral longitudinal trunks, connected by transverse commissures in the prothorax and eighth abdominal segment; the mesothoracic



Figs. 25-28. *Chartocerus subaeneus*. 25, Female metasoma: T7, T8 and epiproct. 26, Male genitalia and eighth sternum. 27, Fourth instar larva: cephalic skeleton. CSD = common salivary duct; E = epistoma; ES = oesophagus; H = hypostoma; HS = hypostomal spur; IPR = inferior pleurostomal ramus; M = mandible; MA = mandibular acron; MC = mandibular condyle; SPR = superior pleurostomal ramus; T = tentorium (terminology after Vance and Smith 1933). 28, Female pupa, ventral view.

spiracles are larger than the other pairs. The midgut occupies the first 7 abdominal segments; the beginning of a hind-intestinal invagination can also be discerned. Third instar (Fig. 24) 800-900 μ long and 370-450 μ wide; mandibular denticle 10 μ long. The midgut now occupies most of the body cavity, and the hind gut is clearly evident but still disconnected. Respiratory system as in the preceding instars. A pair of large glands can be seen in the prothoracic region. Fourth instar 1000 μ long and 450 μ wide; mandibular denticle 14-16 μ long. It is otherwise similar to the preceding instar. The cephalic skeleton is best seen in cleared specimens of this instar (Fig. 27).

At the end of the fourth instar, the larva emits meconial pellets. The prepupa is milky white, somewhat smaller than the full-grown fourth instar. At 32°C, pupation takes place on the 7th day after oviposition.

The pupa (Fig. 28) is of typical chalcidoid form. On the first day it is entirely pale, sometimes with beginnings of pigmentation on the vertex. On the second day pigmentation appears on the abdomen, and the propodeal triangle becomes evident.

On the third day pigmentation spreads to all parts of the body, and all imaginal organs can be discerned. On the fourth day the pupa is entirely black. Adult emergence occurs 6 or 7 days after pupation.

BIOLOGY

Chartocerus subaeneus is a direct hyperparasite, attacking only parasitized, mummified mealybugs. It develops ectoparasitically upon well-developed larvae or pupae of its primary hosts within the mummified mealybug. Although occasional mummies were found to contain two *Chartocerus* eggs, development is always solitary and only one adult hyperparasite emerges from each secondary host. Prior to parasitization, the female usually host-feeds on its primary hosts. Reproduction is deuterotokous: virgin females give rise to female progeny, and males are rather rare. Random sampling of lab cultures yielded 5.25% males. However, males were observed to court females and tried to mate with them.

Adult Behavior: Predatory Host-Feeding and Oviposition

Female *C. subaeneus* wasps are positively phototactic, negatively geotactic, and positively thigmotactic, tending to enter crevices, folded leaves, mealybug egg masses and empty mummies.

Upon encountering a mummified mealybug, the female wasp walks around and over it and taps it with the tips of her antennal clubs. Some hosts are accepted rapidly (1-2 min.), but for others more prolonged examination is needed before a decision to accept or reject the host is reached. When a mummy is found acceptable, the wasp turns around, with her caudal end directed towards it, and examines it with her ovipositor. If all is well, this again may take only 2 minutes or less; otherwise, the examination is prolonged until the host is accepted or rejected. When the site of attack is selected, the wasp appears to lean with her antennae upon the substrate, her body pressed hard to the mummy, and starts drilling a host-feeding hole. During drilling, the entire body is seen to tremble, and the ovipositor may be partly withdrawn and re-inserted. An inexperienced wasp may drill for 12-23 min., whereas wasps with several days' experience accomplish the task in 10-14 min. After the ovipositor is withdrawn, the wasp examines the mummy for a few seconds with her antennae, locates the hole, and commences feeding. Immediately after feeding is completed, the wasp turns around and drills again in the same area, searches with her ovipositor inside the mummy, and lays an egg. Drilling and oviposition take 8-13 min., after which the wasp moves on to another mummy, examines it with her antennae and ovipositor, drills and oviposits in it without further host-feeding. In two hours a wasp may construct a feeding hole, host-feed, and lay about 3 eggs in as many mummies.

Most wasps went through this cycle of host-feeding and oviposition. However, a few departed from it and laid an egg before host-feeding or, when offered honey, fed upon it before laying an egg.

For successful drilling by *C. subaeneus*, the secondary host mummy has to be secured to the substrate. In nature, parasitized mealybugs tend to hide in crevices and adhere to the substrate prior to mummification.

Two types of host-feeding were observed: a short feeding period of 1-4 min., and a longer one

lasting 12.5 - 22 min. Both were always followed by oviposition upon the same host. It appears that the short host-feeding period serves mostly as a stimulant to oviposition, whereas the longer period serves to satisfy the wasp's nutritional requirements for continued oviposition. Extensive feeding may result in death of the primary host. Indeed, some of the mealybug mummies in our *C. subaeneus* cultures did not yield any parasite, primary or secondary, and comparison with mummies exposed to *T. peregrina* alone indicated that the incidence of such mortality was significantly higher in the presence of the hyperparasite than in its absence (19.1% vs. 7.3%, respectively, $p=0.05$).

Host Range

In single-choice laboratory experiments, females of *C. subaeneus* readily examined, host-fed and oviposited upon the following encyrtid primary hosts, on which their progeny developed to maturity: *Anagyrus fusciventris* (Girault), *Anagyrus pseudococci* (Girault), *Leptomastidea rubra* Tachikawa and *Tetracnemoidea peregrina* (Compere) in the long-tailed mealybug, *Pseudococcus longispinus* (Targioni Tozzetti); *Anagyrus pseudococci* (Girault), *Clausenia josephi* Rosen and *Leptomastix dactylopii* Howard in the grape mealybug, *Planococcus vitis* (Niedzielski); *Anagyrus pseudococci* (Girault) in the citrus mealybug, *Planococcus citri* (Risso); and *Clausenia purpurea* Ishii in the citriculus mealybug, *Pseudococcus citriculus* Green.

The wasps examined, inserted their ovipositor into and host-fed upon the encyrtid *Microterys flavus* (Howard) in the brown soft scale, *Coccus hesperidum* L. (Homoptera: Coccidae), and *Aphidius* sp. (Hymenoptera: Aphididae) in mummies of the oleander aphid, *Aphis nerii* Boyer de Fonscolombe (Homoptera: Aphididae), but no eggs were laid upon these hosts. Puparia of *Drosophila melanogaster* were ignored by the wasps.

Fecundity

Materials and methods.— In order to determine whether the wasps were pro- or synovigenic, several newly-emerged females were dissected before they had the chance to either feed or oviposit, and their ovaries were examined.

Cards bearing 20-30 mummies of the long-tailed mealybug, containing *T. peregrina*, were placed in small plastic cups. A silk cover was fastened to the cup by means of a plastic lid in which a large hole was bored for ventilation, and some honey was

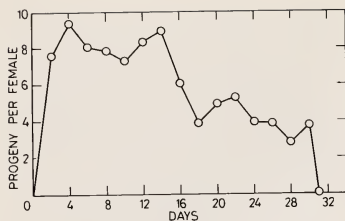


Fig. 29. *Chartocerus subaeneus*, daily progeny production at 28°C , $>50\%$ RH (initial $n = 6$).

streaked on the inside of the cup. Six newly-emerged female wasps were placed singly in these oviposition cups, at $28\pm 1^{\circ}\text{C}$, $>50\%$ RH and a photoperiod of 12L:12D, and were transferred to new cups, without anaesthetization, at daily intervals throughout their life. Following oviposition, the cups were kept at $28\pm 1^{\circ}\text{C}$, and emergence of *C. subaeneus* progeny was recorded daily.

Results.— Dissection of 10 newly-emerged females revealed that each ovary comprised 4 ovarioles, each containing one fully-developed egg.

Oviposition commenced upon the day of emergence and continued evenly throughout the female's life span, declining somewhat in the last days (Figs. 29, 30). On average, a female laid 57% of her eggs during the first half of her life.

Fecundity was rather high. The females lived for a mean of 24.9 days (17-30), and oviposited

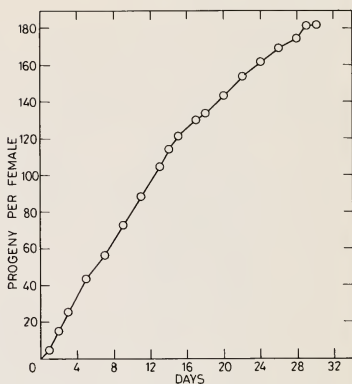


Fig. 30. *Chartocerus subaeneus*, cumulative progeny production at 28°C , $>50\%$ RH (initial $n = 6$).

throughout that period (average 24.3 days). Daily progeny production averaged 6.8, and mean total fecundity was 163.3 progeny per female (range 125-192).

FACTORS AFFECTING ADULT LONGEVITY

Photoperiod

Materials and methods.— Batches of 15 or more newly-emerged female wasps were kept in small plastic cups (as in Fecundity, above), with some honey as food, at $28\pm 1^{\circ}\text{C}$ and $>50\%$ RH, under 24D, 12L:12D and 24L. Mortality was recorded daily.

Results.— As shown in Fig. 31, the longevity of adult females was similar at 12L:12D and 24L, but their longevity was prolonged considerably at 24D. This may have resulted from reduced activity in darkness.

Relative humidity

Materials and methods.— To assess the moisture requirements of *C. subaeneus*, the longevity of female wasps was compared under 0% and 50% RH, as suggested by Bartlett (1962). Two small plastic cups, each with a silk cover held in place by a plastic lid with a large hole in it, were sealed and fastened to one another, lid to lid, with Permagum® cords (Virginia Chemicals, U.S.A.) so that they

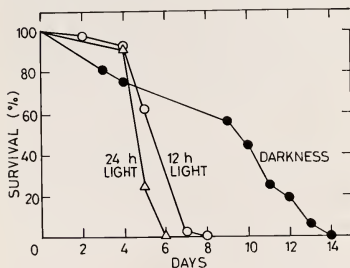


Fig. 31. *Chartocerus subaeneus*, effect of photoperiod on survival of adult females at 28°C , $>50\%$ RH, with honey as food.

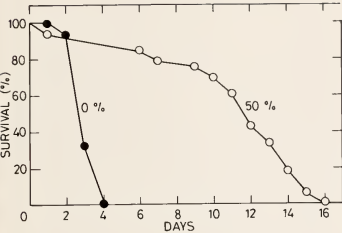


Fig. 32. *Chartocerus subaeneus*, effect of relative humidity on survival of adult females (black circle n = 47; open circle n = 45).

formed a closed unit. Relative humidity was controlled by placing in the bottom cup dry P_2O_5 for 0% RH or a solution of 62.5 gr KOH in 100 cc water for 50% RH (Peterson 1964). Some honey was streaked in the upper cup, and after the system was allowed to reach an equilibrium for 48 hours at $28 \pm 1^\circ C$, it was opened momentarily and several newly-emerged female wasps were placed in the upper cup. Forty-seven wasps were used at 0% RH, 45 at 50% RH. The units were kept in the dark, at $28 \pm 1^\circ C$, and mortality was recorded daily.

Results.— *C. subaeneus* is rather susceptible to low relative humidity (Fig. 32). At 0% RH, 50% mortality was reached on the third day and the last survivors died on the fourth day; whereas at 50% RH, 50% mortality was reached on the 12th day and the last survivors died on the 16th day.

Nutrition

When batches of 10 or more newly-emerged female wasps were kept at $28 \pm 1^\circ C$ and $>50\%$ RH, with no food or water and in the absence of hosts, they all died within 3 days. Provision of water for drinking did not prolong their life span.

Provision of pollen in addition to honey, at 12L:12D and in the absence of hosts, shortened the longevity of the wasps considerably in comparison to that on honey alone: 50% mortality was reached on the 4th day, and the last survivors died on the 6th day (compare with Fig. 31, 12L:12D for survival on honey alone).

In all the experiments with honey in the absence of hosts, the longevity of adult female wasps was

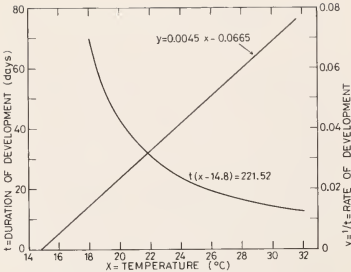


Fig. 33. *Chartocerus subaeneus*, effect of temperature on rate and duration of development.

considerably lower than in the presence of hosts. The 6 females used in the fecundity experiment (Fig. 29) had a mean life span of 24.9 days, whereas under similar conditions but without hosts their mean life span was 6.9 days and they never survived for more than 16 days (see Figs. 31, 32). Predatory host-feeding must have a pronounced effect in prolonging the life span of *C. subaeneus*.

Effect of Temperature on Rate of Development

Materials and methods.— Cards bearing long-tailed mealybug mummies, containing *T. peregrina*, were exposed to females of *C. subaeneus* for 24 hours at room temperature, and were then placed in incubators at 24° , 25° , 28° and $32^\circ C$. Emergence of adult *C. subaeneus* progeny was recorded daily.

The equilateral hyperbola equation, based on the assumption that the product of developmental time and temperature above a certain threshold is a constant for any given species, is a convenient way of expressing the effects of temperature on the duration of development of insects (Bodenheimer

Table 1. Effect of temperature on duration of development of *C. subaeneus*.

Temperature (°C)	Duration of development (days)		
	N	Range	Average \pm SD
24	11	23-25	23.92 \pm 0.67
25	34	18-27	21.77 \pm 2.30
28	52	15-19	16.39 \pm 0.71
32	43	12-14	12.86 \pm 0.64

1958). The hyperbola equation for *C. subaeneus* was calculated as follows: rates of development at the various constant temperatures tested were obtained as the reciprocals of the developmental periods; the linear regression ($y = a + bx$) of developmental rate on temperature was then calculated by the method of least squares; the parameters of the equilateral hyperbola (thermal constant, ThC, and the developmental threshold, c), were then obtained from the identities $ThC = 1/b$; $c = a/b$.

Results.—The results are presented in Table 1. The regression of the rate of development on temperature and the corresponding equilateral hyperbola for *C. subaeneus* are presented in Fig. 33. The calculated developmental threshold was 14.8°C and the thermal constant was 221.52 days-degrees. Since *C. subaeneus* developed normally at 32°C, the upper temperature threshold must have been rather high.

DISCUSSION

The oviposition behavior of *C. subaeneus* is similar to that of other Signiphoridae. Other species have been observed to require lengthy periods for oviposition (Woolley and Vet 1981, Agekyan 1968, DeBach et al. 1958, Clausen 1924), and other species appear to require a period of host-feeding before oviposition can occur (see Woolley and Vet 1981, Quezada et al. 1973). Oviposition upon the same individual hosts which were used for host-feeding was observed in all of these cases, and in *C. subaeneus* it is the most common behavioral sequence.

The biology of only one other species of *Chartocerus*, *C. elongatus*, has been reported in any detail (Clausen 1924). Like this closely-related species, *C. subaeneus* is an obligate hyperparasite. In fact, we know of no cases (published or unpublished) in which it is clear that a *Chartocerus* species develops as a primary parasite. This is in contrast to *Signiphora*, in which some species are primary and others are hyperparasitic. In our experiments, *C. subaeneus* was strictly a solitary parasite, but Clausen (1924) found *C. elongatus* to be gregarious in attacking primary parasites of *Pseudococcus maritimus* (Ehrhorn).

The *C. subaeneus* female emerges with several well-developed eggs that she may deposit on the first day of her adult life, and develops the rest continually during her lifetime. Predatory host-feeding or other sources of proteinaceous nutrition are not required, other than as a stimulant for the

beginning of oviposition, but are presumed to be necessary for continuous egg production in later stages.

As has been reported for other ectophagous hyperparasites (Sullivan 1987), *Chartocerus subaeneus* appears to be rather polyphagous, capable of attacking various encyrtid primary parasites within various mummified mealybugs. It may utilize other primary parasites developing in yet other homopterous hosts for host-feeding. This may enhance its survivorship in the absence of suitable hosts for oviposition.

We were intrigued to find that the egg of *C. subaeneus* bears an elongate projection similar to that reported for *C. elongatus* by Clausen (1924). Such a projection has not been reported for any *Signiphora* species to our knowledge, and it may have systematic significance.

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A Review of the Genus *Hingstoniola* (Hymenoptera: Sphecidae: Crabronini)

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Abstract.—*Niwoh* Tsuneki, 1984, is synonymized with *Hingstoniola* Turner and Waterston, 1926, and *Niwoh tarsata* Tsuneki, 1984, is transferred to the latter genus. An updated generic description of *Hingstoniola* is provided and differences from related genera are discussed. A section containing *Hingstoniola* in Bohart and Menke's key to Crabronini is revised. A key to males of the three included species is provided. *Hingstoniola pagdeni* is first recorded from Thailand.

Hingstoniola is a little-known genus of crabronine wasps, endemic to the Oriental Region. It was established by Turner and Waterston (1926) as a subgenus of *Crabro* for their new species *duplicata* from Sikkim, northern India. Pagden (1934) described a second species, *fimbriata* (nec Rossi, 1790), from Malaysia. Pate (1944) raised *Hingstoniola* to genus and suggested it was a member of his *Foxita* complex. Leclercq included it in his keys to the genera of Crabroninae (1951, 1954) and described the first female (1963). Court in Bohart and Menke (1976:417) partially redescribed the genus and summarized the available information. Most of these treatments are either incomplete or contain factual errors. In 1984a, Tsuneki described a new genus *Niwoh*, which is clearly a synonym of *Hingstoniola*. This paper is an attempt to correct inaccuracies and omissions and to present an updated review of the genus.

The following abbreviations are used for institutions in which the material is housed: BMNH: British Museum (Natural History), London, England (now The Natural History Museum); CAS: California Academy of Sciences, San Francisco, California, USA; USNM: United States National Museum of Natural History (= Smithsonian Institution), Washington, D.C., USA.

Genus **HINGSTONIOLA** Turner and Waterston

Hingstoniola Turner and Waterston, 1926:189 (as a subgenus of *Crabro*). Type species: *Crabro duplicatus* Turner and Waterston, 1926:190, by monotypy.

Niwoh Tsuneki, 1984a:20. Type species: *Niwoh tarsatus* Tsuneki, 1984a:20, by monotypy. Gender: masculine ("Deva King, guardian giant bonze of Budda"). New synonymy.

Synonymy.—An analysis of the original description of *Niwoh* and a subsequent study of the type species of *Hingstoniola* and *Niwoh* convinced us that these two nominal genera are synonyms.

Diagnosis.—*Hingstoniola* is distinguished from other crabronines by the following combination of characters: scapal basin margined dorsally and laterally by a well-defined carina (Fig. 2) and bisected by a vertical carina in males and some females; median lobe of clypeus double-edged (Fig. 1), area between edges concave and delimited laterally by a longitudinal carina on each side; head and thorax with coarse, irregularly reticulating ridges, interspaces microareolate (Fig. 3), hence dull; frons with neither carina nor furrow between midocellus and scapal basin (Fig. 3); and males with flagellum fimbriate anteriorly (Fig. 2), foretarsus conspicuously expanded, and midtibia lacking apical spur.

Description.—Head and thorax with coarse, irregularly reticulating ridges superimposed on microareolate interspaces (Fig. 3); eyes asetose, inner orbits converging below; scapal basin bordered both dorsally and laterally by a well-defined carina (Fig. 2), bisected by vertical carina in males (Fig. 2) and some, but not all, females (Tsuneki, 1984a:24); frons with neither carina nor furrow between midocellus and transverse carina delimiting scapal basin (Fig. 3); orbital foveae present (Fig. 3); ocellar: triangle slightly broader than high (Fig. 3); postocular sulcus present, foveolate, delimited by carina, or absent; gena simple; occipital carina flanged, foveate, joining or ending just short of hypostomal carina; antennal sockets contiguous to each other, contiguous to or separated from orbit; scape bicarinate, carina well defined from base to

apex; male flagellum with 11 articles, modified, with anterior rather than ventral fringe of fimbriae (Fig. 2) (flagellum fimbriate in *pagdeni* and *tarsata*, and row of long, appressed setae on the flagellum of the holotype of *duplicata* apparently originally erect); flagellomeres I-X with raised, carina-like structure that has median, longitudinal slit (Figs. 4 and 5); slit bottom with micropores (we observed a carina on flagellomeres VI-X in *duplicata*, but could not study its microstructure); median lobe of clypeus double-edged (Fig. 1), area between edges concave and delimited laterally by a longitudinal carina on each side; palpal formula 6 + 4; mandibular apex tridentate in female (Fig. 1), bidentate in male; externoventral (= posterior) margin entire, inner margin with tooth on basal half; pronotal collar carinate anteriorly, notched medially, angulate laterally; scutum without anterolateral transverse carinae; notauli and admedian lines present or obscured by coarse sculpture; prescutellar sulcus well developed and foveate; axillae moderately broadened; scutellum margined laterally and posteriorly; metanotum coarsely sculptured; mesopleuron with postspiracular carina, omaulus and acetabular carina continuous; verticaulus present; sternaulus, hypersternaulus, and mesopleuraulus absent; propodeum coarsely sculptured, enclosure areolate; lateral propodeal carina well developed; male legs with fore- and midtarsi modified, forefemoral venter with longitudinal carina; midtibial spur present in female, absent in male; recurrent vein joining submarginal cell beyond middle of cell's hindmargin; jugal lobe slightly longer than submedian cell (appears shorter in some specimens); gaster sessile; pygidial plate narrow, concave in female, absent in male.

Systematics.—A study of cladistic relationships of *Hingstoniola* to other Crabronini is beyond the scope of the present paper. Instead, comparisons are made between *Hingstoniola* and other genera in which the scapal basin is delimited by a carina both dorsally and laterally. This conspicuous feature, found only in *Enoplolindenius* (New World), *Foxita* (Neotropical), *Hingstoniola*, and *Vechtia* (Oriental), is clearly derived within the Sphecidae and may be a synapomorphy of these genera. The goal is to facilitate recognition of *Hingstoniola* and to review the distribution of taxonomically important characters.

Unlike *Hingstoniola*, the scapal basin in the other three genera is not bisected by a vertical carina; the

clypeal margin is single-edged; the head and thorax are shiny, not reticulate (head matte in *Foxita leydensis* Leclercq); the frons has a carina between the anterior ocellus and the scapal basin (reduced in *Foxita castrica* Leclercq); and the male flagellum is not fimbriate anteriorly but has a ventral setal fringe in some *Enoplolindenius* and some *Foxita*. The male foretarsus is conspicuously expanded in *Hingstoniola* and some *Enoplolindenius*, simple in the other two genera.

Hingstoniola, *Foxita*, and *Vechtia* differ from *Enoplolindenius* in having the mandible tridentate in the female and bidentate in the male, palpal formula 6 + 4, scutum without anterior transverse carinae, and female pygidial plate narrow, concave. *Enoplolindenius* has the mandibular apex simple; palpal formula 6 + 3; scutum with a distinctive carina that extends outwards from each notaulus parallel to the scutal foremargin; female pygidial plate broad, flat; and male midtibial spur present or absent.

Hingstoniola is further separated from *Foxita* in having the following: the occipital carina does not form a complete circle, but joins the hypostomal carina or nearly so; and the hypersternaulus, mesopleuraulus, and male midtibial spur are absent. In most *Foxita* (in part from Leclercq, 1980), the occipital carina forms a complete circle separated from the hypostomal carina (evanescent mesoventrally in females of *beieri* Leclercq, *galibi* Pate, and *nabeieri* Leclercq, and subtant to the apex of V-shaped hypostomal carina in *atorai* Pate species group), the hypersternaulus and mesopleuraulus are present or absent, and the male midtibial spur is present. In addition, the recurrent vein joins the submarginal cell beyond the midlength of the cell's hindmargin in *Hingstoniola*, before to beyond middle in *Foxita* (not always near middle as stated by Court).

Hingstoniola differs from *Vechtia* in having the following: the carina that borders the scapal basin dorsally is not lamellate, the occipital carina joins the hypostomal carina or nearly so, the sternaulus is absent, and the recurrent vein joins the submarginal cell beyond the middle of the cell's hindmargin. In *Vechtia*, the scapal basin carina is expanded dorsally into a triangular, downcurved lamella, the occipital carina forms a complete circle separated from the hypostomal carina, the sternaulus is present, and the recurrent vein joins the submarginal cell at or near the middle of the

cell's hindmargin. The male midtibial spur is absent in *Vectitia rugosa* (F. Smith), but present in *V. prerugosa* Leclercq (holotype examined).

The following replaces couplets 10-12 in the key to genera of Crabronini by Bohart and Menke, 1976: 374. The figure numbers refer to the illustrations in their book.

Three species are currently included in *Hingstoniola*: *duplicata* (Turner and Waterston), *pagdeni* Leclercq, and *tarsata* (Tsuneki). The female of *duplicata* is unknown and that of *tarsata* is not available for study. The differences between the males are summarized in the second key below.

KEY TO GENERA OF CRABRONINI WITH DORSALLY AND LATERALLY MARGINED SCAPAL BASIN

10. Scutum with transverse anterolateral carinae (fig. 121 H); mandibular apex simple; female pygidial plate broad, flat, coarsely punctate; New World *Enoplolindenius* Rohwer
- Scutum without transverse anterolateral carinae; mandibular apex tridentate in female, bidentate in male; female pygidial plate markedly narrowed, concave 11
11. Dorsal carina of scapal basin expanded medially into a downcurved, triangular lamella (fig. 122 I); sternaulus present; Oriental *Vectitia* Pate
- Dorsal carina of scapal basin nonlamellate medially; sternaulus absent 12
12. Head and thorax with coarse, reticulate sculpture; occipital carina not a complete circle, joining hypostomal carina or ending just short of it (hypostomal carina U-shaped); median clypeal lobe double-edged, area between edges concave and delimited laterally by longitudinal carina on each side; male flagellum with anterior fringe of fimbriae; male foretarsus conspicuously expanded; Oriental *Hingstoniola* Turner and Waterston
- Head and thorax without reticulate sculpture; occipital carina a complete circle (evanescent mesoventrally in some females), well separated from hypostomal carina (if latter U-shaped) or sub tangent to it (if V-shaped); median clypeal lobe single-edged; male flagellum without anterior fringe of fimbriae; male foretarsus simple; Neotropical *Foxita* Pate

KEY TO MALES OF *HINGSTONIOLA*

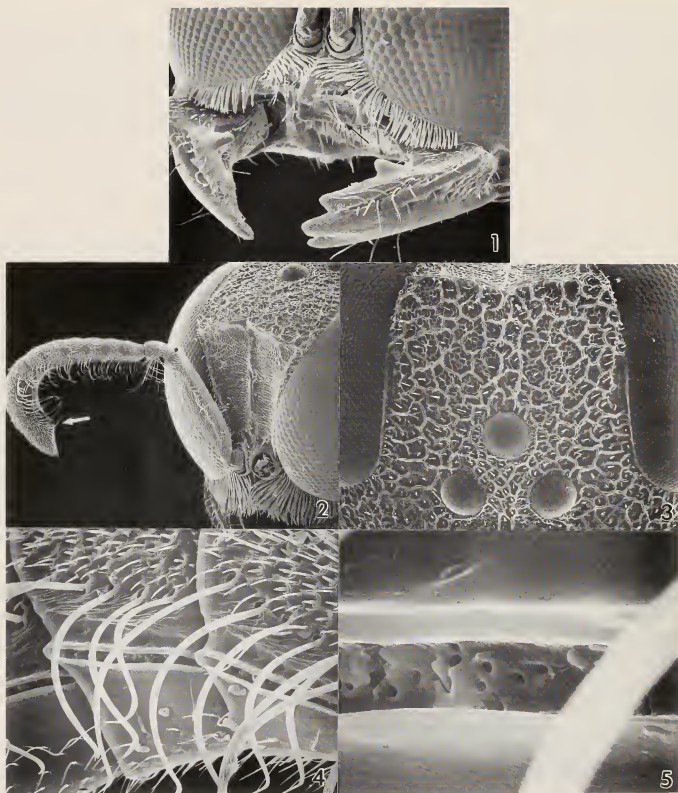
1. Median clypeal carina expanding to form a raised, blunt tooth that extends beyond clypeal margin; flagellomere XI with no basal tubercle; metanotum undivided mesally; forefemoral venter angulate at basal one-third of length, angle with cluster of erect setae; foretarsomeres I-III without well-defined color pattern, each with one long seta at anterodistal angle (= side away from articulation of tarsomere II); foretarsomere I acutely angulate anterodistally *duplicata* (Turner and Waterston)
- Median clypeal carina not expanding into median projection (free margin of clypeal lobe truncate mesally); flagellomere XI with sharp tubercle basoventrally (Fig. 2); metanotum anteromedially with lunate, sharply margined area; forefemoral venter with a few stiff, erect, sparsely spaced setae, not angulate at basal one-third; foretarsomeres I-III with conspicuous black pattern, anterior margins (= side away from tarsal articulations) with long, curved fimbriae except basally; foretarsomere I rounded anterodistally 2
2. Anterior margin of foretarsomere I about 1.3 x posterior margin; midlengths of midtarsomere II and midtarsomere III equal to their respective apical widths *tarsata* (Tsuneki)
- Anterior and posterior margins of foretarsomere I about equal in length; midlength of midtarsomere II 0.9 x apical width, of midtarsomere III 0.6 x apical width *pagdeni* Leclercq

DISCUSSION OF SPECIES

Hingstoniola duplicata (Turner and Waterston)

Crabro duplicata Turner and Waterston, 1926:190, male, incorrect original termination. Holotype: male, India: Sikkim: Kalimpong, 1220 m, 27 Mar 1924, R.W.G. Hingston collector (BMNH), examined. — Pagden, 1934:482 (comparison with *Crabro fimbriatus*). — As *Hingstoniola duplicata*: Pate, 1944:377 (new combination); Leclercq, 1951:32 (type examined), 1954: 218 (listed); Bohart and Menke, 1976: 417 (listed).

This distinctive species is known only from the holotype male, which is in poor condition. The labiomaxillary complex and right antenna are missing, and the apical two flagellomeres of the remaining antenna are disjointed. Apparently as a result of improper preservation, the eye surface is irregularly ridged, the ocelli are collapsed (alveolate in appearance), the wings are dirty, and many setae, including those on the antenna, are appressed



Figs. 1-5. *Hingstoniola pagdeni* Leclercq. 1, Female clypeus obliquely from below (x 60), with arrows showing the upper and lower clypeal edges. 2, Male head and antenna obliquely from the side (x 47), with arrow showing tubercle on flagellomere XI. 3, Male frons in top view (x 79). 4, Flagellomeres VI, VII, and part of VIII (x 470). 5, Slit of flagellomere VII (x 3350).

to the integument. Fortunately, males of *duplicata* are easily distinguished from those of *pagdeni* and *tarsata* by the characters given in the key. Females will probably be most readily recognized by the undivided metanotum.

Turner and Waterston (1926) incorrectly described the forefemur of the male *duplicata* as having a ventral spine at one third of its length. In reality, the femur is angulate, with a cluster of erect setae at the angle. Pagden (1934) thought that *duplicata* differed from *pagdeni* in lacking the row of erect fimbriae on the flagellum, but the fimbrial row in the type is probably merely matted down.

Hingstoniola pagdeni Leclercq

Crabro fimbriata Pagden, 1934:482, male, incorrect original termination. Holotype: male, Malaysia: Kedah: Bukit Panchar, 4 June 1930, H.T. Pagden collector (BMNH), examined. Nec *Crabro fimbriatus* Rossi, 1790. — Pagden, 1934:476 (as prey of *Cerceris langkasukae*). — In *Hingstoniola*: Leclercq, 1951:52 (new combination, listed).

Hingstoniola pagdeni Leclercq, 1954:218, replacement name for *Crabro fimbriata* Pagden. — Leclercq, 1963:47 (Malaysia: Kuala Lumpur; description of female); Bohart and Menke, 1976: 418 (listed).

Crabro parviornatus Cameron: Leclercq, 1951:52, nomen nudum (Borneo: Kuching).

The holotype of *pagdeni* is also in poor condition: it lacks the flagella and gaster. The head is missing in the male labeled as *parviornatus* Cameron (the only specimen studied by Court in Bohart and Menke, 1976).

This species is very similar to *tarsata* (see the latter for discussion). The holotype of *pagdeni* was collected as prey of a *Cerceris* that Pagden described as *langkasukae* on p. 476, but called *spiniventris*, a nomen nudum, in the holotype data of *pagdeni* on p. 486 (Krombein, 1981:30, synonymized *langkasukae* with *bidentula* Maidl, 1926). Pagden himself reported that this was an unusual prey record since the other females were taken with buprestids, the normal prey of this species.

Hingstoniola pagdeni was described from Bukit Panchar, Kedah Province, Malaysia, and subsequently recorded from Kuching, Borneo (Leclercq, 1951) and Kuala Lumpur, Malaysia (Leclercq, 1963). An additional, northernmost locality is Doi Suthep mountain in Chiang Mai Province, Thailand (4 females, 3 males, 1-2 May 1989, W.J. Pulawski collector, CAS). These specimens were flying around bushes in the sun in a little stream valley not far from the Wat Phra That temple.

Hingstoniola tarsata (Tsuneki), new combination

Niwoh tarsata Tsuneki, 1984a:20, male, female, incorrect original termination (correctly spelled *tarsatus* on p. 25). Holotype: male, Philippines: Mindanao: Cagayan de Oro: Makahambus Cave, 15 Aug 1980, T. Murota collector (originally K. Tsuneki collection, now USNM), examined. — As *Niwoh tarsatus*: Tsuneki, 1984b: 2 (Philippines), 30 (in key).

In addition to the characters given in the key, *tarsata* and *pagdeni* differ in the shape of the clypeus and the flagellar slits. The median clypeal carina is flattened apically to form a triangular bevel in *tarsata*, whereas *pagdeni* has no bevel. The width of a flagellar slit is about two fimbrial diameters in *tarsata* and about one diameter in *pagdeni* (Figs. 4, 5). So far, *tarsata* is known only from Mindanao Island, Philippines.

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CONTENTS

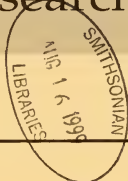
(Continued from front cover)

MENKE, A.S. Mole cricket hunters of the genus <i>Larra</i> in the New World (Hymenoptera: Sphecidae, Larrinae)	175
NORDEN, B.B., K.V. KROMBEIN, and B.N. DANFORTH. Taxonomic and bionomic observations on a Floridian panurgine bee, <i>Perdita (Hexaperdita) graenicheri</i> Timberlake (Hymenoptera: Andrenidae)	107
PULAWSKI, W.J. and H.K. COURT. A review of the genus <i>Hingstoniola</i> (Hymenoptera: Sphecidae: Crabronini)	255
QUELLER, D.C., J.E. STRASSMANN, and C.R. HUGHES. Genetic relatedness and population structures in primitively eusocial wasps in the genus <i>Mischocyttarus</i> (Hymenoptera: Vespidae)	81
ROSEN, D., Y. ARGOV, and J.B. WOOLLEY. Biological and taxonomic studies of <i>Chartocerus subaeneus</i> (Hymenoptera: Signiphoridae), a hyperparasite of mealybugs	241
STOLTZ, D. and J.B. WHITFIELD. Viruses and virus-like entities in the parasitic Hymenoptera	125
INSTRUCTIONS FOR AUTHORS	Inside back cover

563
568X
Ent



Journal of Hymenoptera Research



Volume 2, Number 1

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CONTENTS

BROTHERS, D. J. and J. M. CARPENTER. Phylogeny of Aculeata: Chrysidoidea and Vespoidea	227
DAVIDSON, D. W. and D. McKEY. The evolutionary ecology of symbiotic ant-plant relationships	13
GENISE, J. F. and L. S. KIMSEY. Revision of the South American thynnine genus <i>Elaphroptera</i> Guerin-Meneville (Hymenoptera: Tiphidae)	195
HERATY, J. M., D. P. WOJIC and D. P. JOUVENAZ. Species of <i>Orasema</i> parasitic on the <i>Solenopsis saevissima</i> -complex in South America (Hymenoptera: Eucharitidae, Formicidae)	169
HEYDON, S. L. <i>Syntomopus</i> Walker: the Nearctic species with a review of known host associations (Hymenoptera: Pteromalidae).	107
KAZENAS, V. L. and B. A. ALEXANDER. The nest, prey and larva of <i>Entomosericus kaufmani</i> Radoszkowski (Hymenoptera: Sphecidae)	221
de MELO, G. A. R. and L. A. de O. CAMPOS. Nesting biology of <i>Microstigus myersi</i> Turner, a wasp with long-haired larvae (Hymenoptera: Sphecidae, Pemphredoninae)	183
MENKE, A. S. A new species of <i>Apocharips</i> from Costa Rica (Hymenoptera: Cynipoidea, Charipidae)	97
PIEK, T. New neurotoxins from venom of aculeate Hymenoptera: a contribution to the knowledge of stinging behavior	101
RASNITSYN, A. P. Archaeoscolinae, an extinct subfamily of scoliid wasps (Insecta: Vespida = Hymenoptera: Scoliidae)	85
SHAW, S. R. Systematic status of <i>Eucystomastax</i> Brues and characterization of the Neotropical species (Hymenoptera: Braconidae, Rogadinae)	1
TOGASHI, I. Sawflies of the genus <i>Perineura</i> Hartig from Japan (Hymenoptera: Tenthredinidae)	189
WARD, P. S. Systematic studies on <i>Pseudomyrmex</i> acacia-ants (Hymenoptera: Formicidae: Pseudomyrmecinae)	117
SCIENTIFIC NOTE	
WILLINK, A. AND A. R. ALSINA. On <i>Odynerus rachiphorus</i> Schletterer, a Masarinae (<i>Trimeria</i>), not a Eumeninae (Hymenoptera, Vespidae)	303

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Fig. 1. Color habitus of *Aleiodes melanopterus* (Erichson) female, oblique antero-lateral view.

Systematic Status of *Eucystomastax* Brues and Characterization of the Neotropical Species (Hymenoptera: Braconidae: Rogadinae)

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Abstract.— *Rogas melanopterus* Erichson is found to be the oldest available name for *Eucystomastax bicolor* Brues, the type-species of *Eucystomastax* Brues. This distinctive Neotropical species has six available species names, and has been placed in three different genera: *Rogas*, *Macrostomion*, and *Eucystomastax*. Possible placements in *Rogas* or *Macrostomion* are evaluated and rejected on phylogenetic grounds, since *Eucystomastax* lacks critical synapomorphies of those lineages. Phylogenetic affinity of *Eucystomastax* with the *Aleiodes*-group is demonstrated. *Eucystomastax* is shown to comprise a monophyletic cluster of species including *Rogas melanopterus* Erichson, *Macrostomion lucidus* Szépligeti, *Aleiodes mexicanus* Cresson, *Rogas politiceps* Gahan, and one newly described species, *Aleiodes flavistigma* Shaw. Full generic validity of *Eucystomastax* is rejected on the grounds that continued recognition as a distinct genus results in a paraphyletic *Aleiodes*, and the *Eucystomastax* lineage can be clearly derived from within North America *Aleiodes*. *Eucystomastax* is reduced in rank to the status of a subgenus of *Aleiodes* comprising those New World species with infumate wings, enlarged oral space, and swollen maxillary palpi. On the basis of synapomorphic color patterns and transitional sculpture characters the Neotropical species are argued to comprise a monophyletic group whose nearest relative is the North American species, *Aleiodes politiceps* (Gahan). Neotropical *Eucystomastax* includes *flavistigma* NEW SPECIES, *lucidus* (Szépligeti), *melanopterus* (Erichson), and *mexicanus* Cresson. A subgeneric diagnosis, key to species, and species descriptions are given for the Neotropical species.

The braconid subfamily Rogadinae comprise a diverse lineage of koinobiont endoparasitoids of lepidopteran larvae (Shaw & Huddleston, 1991). Among species of the tribe Rogadini pupation is internal, within the host cuticle, resulting in a distinctive shrunken caterpillar mummy (Shaw, 1983). The Neotropical rogadine fauna is quite diverse and challenging taxonomically. Although the problem arises in part from the tremendous species richness and the fact that many species are undescribed, equally challenging is the difficult task of sorting out the chaotic taxonomic history of the already named species. The older literature is often difficult to acquire and the types of Neotropical rogadines are mostly scattered around various European and North American museums. Added to this is confusion created by the fact that many of the original generic placements were wrong and have not been corrected in even the most recent catalogues. The purpose of this paper is to clarify the confused history pertaining to the unique Neotropical lineage *Eucystomastax* Brues and to evalu-

ate the phylogenetic affinities and validity of the "genus." This study was initiated in support of a collaborative effort to develop an identification manual for the genera of Neotropical Braconidae, which requires that the systematic status of various genera be clarified.

METHODS

Terminology mostly follows that used by Marsh, Shaw & Wharton (1987) for Braconidae and Marsh (1989) for *Aleiodes*. Microsculpture terminology follows that outlined by Harris (1979). The following abbreviations are used in the diagnoses:

- BL Body length, in dorsal view, excluding antenna and ovipositor.
- FWL Fore wing length.
- F# Flagellomere #.
- MS Malar space.
- EH Maximum eye height.
- EW Maximum eye width.

TW	Temple width.
OS	Oral space, maximum width in anterior view.
OOD	Ocell-ocular distance: shortest distance from eye margin to lateral ocellus.
OD	Ocellus diameter: maximum width of lateral ocellus.
T#	Tergum #.
OL	Ovipositor length.
HBTL	Hind basitarsus length.
HTS	Hind tibial spur length (longest spur).
R#	Radius segment #.

Abbreviations for museums can be found in the Acknowledgments section.

HISTORICAL OVERVIEW OF THE SPECIES *Eucystomastax melanopterus*

One of the commonest and most distinctive elements of the Neotropical rogadine fauna is a large orange and black species with infumate wings, large oral space, and swollen maxillary palpi (Figure 1). The first author to describe this species was Erichson (1848), who named it *Rogas melanopterus*. Although banded wings are fairly common among tropical rogadines, completely infumate wings are rather unusual. In spite of the fact that the specific epithet rather obviously refers to the unusual dark wings of this species, the correct application of this name has long remained obscure.

Szépligeti (1904) described this species as *Macrostomion peruvianum* based on a specimen from Peru. The genus *Macrostomion* Szépligeti had been described four years earlier based on a specimen from New Guinea (Szépligeti, 1900). Szépligeti (1906) described another closely related species, *Macrostomion lucidus*, based on a specimen from Bolivia. Although the South American species differ from the New Guinean *Macrostomion* in a number of characters, Szépligeti grouped the species together in one genus based on the swollen maxillary palpus.

Cameron (1911) described the species three more times, based on three specimens from British Guiana (Guyana). He placed this species in *Rhogas* [= *Rogas*], but gave no explanation for his generic placement. Cameron was the first author to treat a

series of specimens (two females and one male), and although the variation presented was very slight, he elected to recognize each of these as a separate species (*Rhogas rufithorax*, *Rhogas fortipalpis*, and *Rhogas forticarinatus*). The characters used by Cameron to separate these "species" were very slight differences in color and sculpture, which are now recognized to fall within the range of normal infraspecific variation.

Brues (1912) described this species as a new genus and species, *Eucystomastax bicolor*, based on a single male specimen from Brazil. Brues noted a general similarity in habitus to *Rhogas* [= *Rogas*], yet he concluded that the species must be placed in a separate genus because of its "dilated palpi." He noted that certain other rogadine genera also have similarly modified palpi (*Macrostomion* Szépligeti, *Pelecystoma* Wesmael, and *Cystomastax* Szépligeti). However, he observed that *Macrostomion* and *Pelecystoma* both have "flattened or leaf-like" dilations of the palpi, therefore precluded relationship with those genera. He noted that *Cystomastax* has slit-like metathoracic spiracles and a petiolate metasoma, and distinguished *Eucystomastax* as a separate genus on the basis of its round metathoracic spiracles and sessile metasoma.

Subsequent to Brues' study, virtually no studies have evaluated this taxon. Shenefelt (1969) studied and redescribed the New Guinean type-species of *Macrostomion* (*Macrostomion bicolor* Szépligeti), but he did not study or discuss the Neotropical species that Szépligeti (1906) had placed in this group. Shenefelt (1975) cataloged the world fauna of Rogadinae, but his treatment of species is largely a literature compilation and does not address the difficult taxonomic problems pertaining to this subfamily. Consequently, the species discussed above, for which the correct specific epithet is *melanopterus* Erichson, is listed in Shenefelt's catalog under six separate species names and classified under three different genera!

PHYLOGENETIC AFFINITIES OF *Eucystomastax* AND EVALUATION OF ITS TAXONOMIC STATUS

Based on the above discussion and comparison

of the holotype specimens, it can now be established that *melanopterus* Erichson is the oldest available name for *bicolor* Brues, the type-species of *Eucystomastax*. Establishing the correct generic placement of *melanopterus* Erichson is, however, a more complex problem requiring a modern perspective on rogadine evolution and classification.

For many years, the correct interpretation of *Rogas* Nees, 1818 and *Aleiodes* Wesmael, 1838 remained obscure, resulting in considerable confusion in the literature. Earlier authors used the names interchangeably, and until just recently the majority of New World rogadine species were classified under *Rogas*. The name *Pelecystoma* Wesmael, 1838 was held distinct for a relatively small grouping of Holarctic species with a swollen maxillary palpus. The situation was clarified by van Achterberg (1982) through a reexamination of the type-species that revealed that *Pelecystoma* is a junior synonym of *Rogas* and that *Aleiodes* is the valid name for many species formerly classified under *Rogas*. Diagnoses for *Rogas* and *Aleiodes* based on a study of Afrotropical and Western Palearctic species were provided by van Achterberg (1991).

Within the tribe Rogadini, two clades predominate. One lineage, here called the *Rogas*-group, is characterized by at least two apomorphies: the presence of a row of flattened setae along the inner margin of the apex of the hind tibia and the presence of an enlarged blunt basal lobe on the tarsal claw. The ovipositor has diagnostic value in that it is usually as long as or longer than the hypopygium and is curved. The *Rogas*-group comprises *Rogas* and several other closely related genera including *Macrostomion*, *Cystomastax*, *Spinaria*, and *Triraphis*. This lineage is cosmopolitan, but it is particularly species-rich in tropical areas where it comprises about 90% of the rogadine fauna (perhaps 300 or more species worldwide, most of which are undescribed). The *Rogas*-group is ecologically distinctive, in that they attack mostly sluggish and slug-like larvae (slow moving, exposed feeders), many of which are gregarious feeders. The known hosts are mostly relatively primitive exposed-feeding macrolepidopterans such as Limacodidae or Zygaenidae, but some parasitize lycaenid or riodinid larvae. Host mummies typically are stuck naturally

to the substrate by host secretions, and no "glue hole" (a ventral hole made by the parasitoid larva to stick the mummy to the substrate) is formed. The exit hole from the host mummy is crude and irregular, usually comprising multiple ragged tears. The hooked pronotal spine of *Spinaria* may be an adaptation for escaping from the host mummy. Mark Shaw (1983) suggested that this group (at least *Rogas*) "arose through an early response to the naked feeding habit in Lepidoptera."

A second major rogadine lineage, here called the *Aleiodes*-group, is also characterized by several apomorphies: non-foveate mesopleural sternaulus, first intercubitus postfurcal relative to the recurrent vein, reduction and loss of the propodeal areola, propodeum with a median carina, and presence of a carinate anterior margin on tergum 2 that typically converges medially into a median percurrent carina, often with an associated polished anteromedial triangular area. In contrast to the *Rogas*-group, the ovipositor is usually much shorter than the hypopygium and is straight. This lineage is also cosmopolitan, but it is particularly species-rich in temperate areas and predominates throughout the Holarctic region. The *Aleiodes*-group comprises at least 200 *Aleiodes* species worldwide (as defined by van Achterberg, 1991) and possibly a few other minor genera including *Tetrasphaeropyx* and *Yelicones*. *Tetrasphaeropyx* is a unique North American lineage comprising one described and at least seven undescribed species, differing from *Aleiodes* only by having a metasomal carapace. The phylogenetic position of *Tetrasphaeropyx* has not been established, therefore it cannot be denied that this small "genus" may only be a specialized offshoot of *Aleiodes*. *Yelicones* is another small genus of worldwide distribution that is currently being revised by D. Quicke. The phylogenetic position of *Yelicones* is controversial, and van Achterberg (1991) has suggested that it should be transferred to another subfamily, the Betylobraconinae. Since *Yelicones* mummifies its host larva and possesses the synapomorphies of the *Aleiodes*-group, it is unlikely that this genus should be removed from the Rogadini (unless the Betylobraconinae are discovered to share this synapomorphy); hopefully Dr. Quicke's study will resolve this issue. With these minor exceptions, the

Aleiodes-group as defined here corresponds almost exactly to the diagnosis of the genus *Aleiodes* provided by van Achterberg (1991). Ecologically, the *Aleiodes*-group is quite distinctive. The known hosts of the *Aleiodes*-group are mostly relatively advanced exposed-feeding macrolepidopterans such as noctuid or geometroid larvae. Mark Shaw (1983) summarized several biological characteristics, which may be construed as further apomorphies of this group. They attack early instars of exposed "macrolepidoptera," attacking the host away from foodplant substrates as readily as on them. They employ venoms that cause short-lived temporary paralysis as a handling device facilitating oviposition, but having no other detectable physiological effect on the host. They oviposit loosely into the host haemocoel as a separate action distinct from injecting venom. They kill the host in a middle instar, forming a somewhat contracted mummy. Lastly, most species cut a ventral "glue hole" in the prothoracic region of the host larva, by which the mummy is attached to the substrate. Shaw (1983) suggested that the lack of "glue holes" in some species is a secondary adaptation to survival in wetland habitats, because loose mummies can float. Because of the tremendous species-richness of the genus, it is difficult to establish the monophyly of *Aleiodes* at the present time. However, it appears that the "glue hole" may be the best autapomorphy for the genus. It is present in all the *Aleiodes* host mummies examined during my studies, but it does not appear to be present in *Yelicones* mummies. Host mummies for *Tetrasphaeropyx* were not available for study.

My preliminary studies, and unpublished studies by P. Marsh, indicate that the *Rogas*-group and the *Aleiodes*-group are sister lineages, based on a unique ultrastructural character. All species examined so far have 2-12 striated accessory spines along the basal 1/8 to 3/4 of the tarsal claw. In contrast, the remaining rogadine genera, such as *Stiropius*, *Polysteniidea*, and *Rhysipolis*, have simple claws without such spines. This is compatible with Whitfield's (1988) supposition that the rogadine parasitoids of leaf-miners (*Stiropius*, *Polysteniidea*, *Viridipyge*) are probably one of the most basal lineages of the tribe.

Eucystomastax belongs to the *Aleiodes*-group, since *melanopterus* possesses the apomorphies indicating placement in this group: absence of a propodeal areola and presence of an undivided median propodeal carina (Fig. 3), presence of a carinate anterior margin along tergum 2 that converges medially into a median percurrent carina with an associated polished anteromedial triangular area (Fig. 6), and a straight ovipositor that is distinctly shorter than the hypopygium (Fig. 7). Furthermore, *melanopterus* lacks the apomorphies of the *Rogas*-group. The apex of the hind tibia lacks a row of flattened setae (Fig. 4) and the tarsal claw lacks a blunt basal lobe (Fig. 5).

The swollen maxillary palpus and large oral space are the only characters by which *Eucystomastax* differs from typical *Aleiodes*. In addition to *melanopterus* Erichson, there are two other valid Neotropical species, *lucidus* Szépligeti and *mexicanus* Cresson, that share these apomorphic traits and are here assigned to *Eucystomastax*. A survey of all known North American *Aleiodes*-group species revealed only one other species that shares apomorphies with Neotropical *Eucystomastax* species. *Aleiodes politiceps* (Gahan) possesses several apomorphic traits indicating that this species is possibly the sister-group of the Neotropical *Eucystomastax* lineage: enlarged oral space (Fig. 2), mesonotum and mesopleuron with predominantly smooth sculpture (Fig. 3), infumated wings (Fig. 1), hind tibia and tarsus densely setose (Fig. 4), pectinate tarsal claws with 4-9 large accessory spines (Fig. 5), and sculpturing of terga 1-3 predominantly longitudinally strigose (Fig. 6).

Brues (1912) has already demonstrated that the swollen maxillary palpus occurs as several distinct character states in different rogadine lineages, so there is a basis for concluding that the character is subject to convergent evolution. One relevant fact that has not been previously emphasized is that the swollen maxillary palpus character is sexually dimorphic in *Rogas*, occurring only in the males, whereas it occurs in both males and females of *Eucystomastax*. The swollen maxillary palpus is generally absent in the *Aleiodes*-group, but in *Aleiodes politiceps* the maxillary palpus is distinctly thickened in both females and males. Although it is not swollen as in *Eucystomastax*, the

thickened condition in *politiceps* may be the first step in a transition series leading to the extreme condition as expressed in *melanopterus* Erichson.

A complete phylogenetic analysis of the *Aleiodes*-group is not possible at the present time, but a preliminary analysis of 14 species indicates that *Eucystomastax* is an offshoot of a relatively apical lineage of New World *Aleiodes* that also comprises the *terminalis* and *parasiticus* species-groups. Because the continued recognition of *Eucystomastax* as a genus would result in a paraphyletic *Aleiodes*, it is necessary that the generic concept of *Aleiodes* be expanded to include *Eucystomastax*, which becomes a junior synonym of *Aleiodes*. However, since *Eucystomastax* is obviously a monophyletic and distinctive lineage and the name is already available, it would seem worthwhile to maintain the name *Eucystomastax* as a valid subgenus for the four Neotropical species and the closely allied North American species, *Aleiodes politiceps*. This is not meant to suggest that all remaining *Aleiodes* can be placed in a single subgenus (*Aleiodes*), only that *Eucystomastax* is a monophyletic group within the genus that is worthy of recognition, but cannot be treated as a valid genus (other *Aleiodes* are considered *incertae sedis* pending further study). As far as is known, *Eucystomastax* does not occur in other biogeographic realms.

In the taxonomic treatment which follows, coverage is limited to the Neotropical species because the North American species of *Aleiodes* are currently being revised by the author, and the species *politiceps* will be fully diagnosed and discussed in that paper.

CHARACTERIZATION OF NEOTROPICAL *Aleiodes* (*Eucystomastax*) SPECIES

Diagnosis: Head and legs mostly black; mesosomal and metasomal color varying from yellowish-brown to bright orange to black; BL 6.75-9.33 mm; FWL 5.50-8.70 mm; flagellum with apical flagellomere terminating in a sharp point; 50-68 flagellomeres; MS/EH 0.12-0.31; TW/EW 0.35-0.75; occipital carina variable: sometimes weak ventrally and not meeting hypostomal carina, sometimes meeting hypostomal carina; OS/

MS 2.15-4.33; OOD/OD 0.70-1.50; face smooth to rugose or rugo-punctate; frons smooth; vertex smooth; temple smooth; maxillary palpus swollen, especially segments 2 and 3, and sometimes 4; propleuron smooth to rugose; mesonotum smooth; notauli scrobiculate to smooth, or sometimes absent; scutellum smooth; mesopleuron smooth; epicnemial carina complete to reduced or absent; sternaulus smooth to absent; propodeum rugose to smooth dorsally, carinate-rugose basally, to entirely smooth; median propodeal carina strong and complete; metasoma comprising 7 visible terga; T1 length/width 0.91-1.18; T2 length/width 0.69-0.82; T3 length/width 0.40-0.54; T1 varying from longitudinally aciculate to rugo-striate to smooth with scattered punctations; T2 varying from longitudinally aciculate to rugo-striate to smooth with scattered punctations; T3 varying from longitudinally aciculate basally, with apical 1/2 smooth, to rugo-striate from extreme base up to entire basal 1/2, otherwise smooth, to entirely smooth with scattered punctations; T4 entirely smooth, but sometimes with scattered punctations; median carina present on T1 and T2; OL/HBTL 0.18-0.96 (unknown for *lucidus*); tarsal claw pectinate, with 4-9 accessory spines becoming gradually smaller basally; HTS/HBTL 0.29-0.35; hind coxa dorsally smooth to punctate; wings deeply infumate; R1/R2 0.37-0.50; R1/recurrent 0.39-0.60; nervulus placement beyond basal vein/nervulus length 1.39-2.67; radiellen cell gradually widening; basella/mediella 0.57-0.85; postnervellus present.

Discussion: *Eucystomastax* species are quite distinctive among the Neotropical rogadine fauna because of their black head and deeply infumate wings (Fig. 1). Although banded wings are rather common among Neotropical rogadines, completely dark wings are rather unusual (probably synapomorphic) and are known only in a few relatively less common *Rogas* species (an evolutionary convergence). The combination of a entirely black head and mostly black wings will easily separate *Eucystomastax* species from most other Neotropical rogadines, even without the aid of a microscope.

Character transformations both in color patterns and morphology (especially mesosomal and metasomal sculpture) suggest that the *melanopterus*

species-group is a monophyletic group whose nearest relative is the North American species, *Aleiodes politiceps* (Gahan). All four Neotropical *Eucystomastax* species have a black head (synapomorphy) and reduced metasomal sculpture from the coarse sculpture seen in *politiceps* (a synapomorphic transition series). It is hypothesized that *flavistigma*, *lucidus*, and *melanopterus* comprise a monophyletic group based on the synapomorphic black metasoma. Of these, *lucidus* has the most extreme apomorphic reductions in body sculpturing. The relationships of these three

species are not yet resolved, but the autapomorphies and more limited distributions of *flavistigma* and *lucidus* suggest that each may be separate offshoots from *melanopterus* or *melanopterus*-like ancestors. The relationships proposed here among *Eucystomastax* species are as follows: *politiceps* + [*mexicanus* + {*flavistigma* + *melanopterus* + *lucidus*}].

Although the hosts of the Neotropical species are not known, the known hosts of North American *politiceps* suggest that moderately large noctuid larvae are the most likely hosts of this group.

KEY TO NEOTROPICAL *EUCYSTOMASTAX* SPECIES

- 1 Metasoma black apically or mostly black (Fig. 1); South America 2
- Metasoma entirely yellowish brown; Mexico *mexicanus* Cresson
- 2 (1) Notauli distinct although smooth (Fig. 3); epinomial carina entirely present 3
- Notauli absent, mesonotum entirely smooth; epinomial carina effaced dorsally or completely absent *lucidus* (Szépligeti)
- 3 (2) Pterostigma yellow *flavistigma*, new species
- Pterostigma black *melanopterus* (Erichson)

Aleiodes (Eucystomastax) flavistigma Shaw, new species

Description of female.—(83 specimens). Head, mesosoma anteriorly, most of legs apically, and mesosoma apically black; mesosoma posteriorly reddish brown; pterostigma and area below pterostigma bright yellow; coxae, propodeum, and T1-6 varying from reddish brown to black; BL 6.75-8.50 mm; FWL 5.50-7.25 mm; flagellum with 55-68F; MS/EH 0.17-0.22; TW/EW 0.44-0.59; occipital carina meeting hypostomal carina; OS/MS 2.40-4.0; OOD/OD 1.25-1.50; face smooth; maxillary palpus swollen, especially segments 2, 3, and 4; propleuron smooth; mesonotum smooth, postero-medially with a short carina; notaulus smooth; sternaulus smooth; epinomial carina complete; propodeum smooth dorsally, carinate-rugose basally; T1 length/width 0.91-1.11; T2 length/width 0.70-0.73; T3 length/width 0.43-0.49; T1

rugose-striate; T2 rugose-striate; T3 smooth; T4 smooth; OL/HBTL 0.22-0.96; pectin of tarsal claw with 4-9 spines; HTS/HBTL 0.29-0.35; hind coxa dorsally smooth; R1/R2 0.37-0.40; R1/recurrent vein 0.39-0.56; nervulus position beyond basal vein/nervulus length 1.56-2.22; basella/mediella 0.57-0.85.

Description of male.—(132 specimens). Essentially as female except flagellum with 50-62F.

Discussion.—This species is morphologically within the range of usual variation for *melanopterus*, but differs dramatically in color patterns. Specimens of *A. flavistigma* are quite distinctive in having the pterostigma and the area of the forewing just below the pterostigma colored bright yellow. Additionally, the light colored areas of the mesosoma and metasoma are dark reddish brown (rather than orange as in *melanopterus*), and greatly reduced in extent (some males are almost entirely black except for the mesopleuron and propodeum which are reddish brown). The only significant

morphological variation between these species is in the surface sculpture of metasomal tergum 3, which is smooth in *A. flavistigma*. Although variable in *A. melanopterus* (and sometimes smooth), the coarse sculpture of tergum 2 often continues onto the basal half of tergum 3 in many *melanopterus* specimens. In spite of little morphological divergence, it seems reasonable to treat this as a separate species because typical *A. melanopterus* occurs sympatrically, with no intermediates. The bright yellow stigma suggests the possibility that *A. flavistigma* is part of a tropical mimicry ring, and it is possible that it evolved from a population of *melanopterus*.

Etymology.—From the Latin *flavus* meaning yellow, and Greek *stigma* meaning spot, in reference to the bright yellow pterostigma.

Distribution.—Brazil, Santa Catarina and Paraná Provinces. Seasonal occurrence from August through March.

Types.—Holotype female: Brazil, Nova Teutonia, 27.11 S, 52.23 W, 300–500m, February 1967, Fritz Plaumann (CNC). Paratypes: 82 females, 132 males, same data as holotype except collection dates ranging from February 1962 through December 1968 (CNC, RMSEL, USNM); 1 female, Brazil, Paraná, Pitangueiras, 24.41 S, 51.46 W, 700m, March 1963, F. Plaumann (MCZ); 1 female, Brazil, Paraná, Bocaiúva do sul, 26.08 S, 49.04 W, 1000m, March 1963, F. Plaumann (MCZ); 2 females, 1 male, Paraná, Prudentópolis, 23–25 February 1969, C. Porter & A. García (MCZ); 1 female, Paraná, Laranjeiras, 25.24 S, 52.23 W, 900m, (no date), F. Plaumann (MCZ); 1 female, 1 male, same data as holotype except 18 January & 25 February 1963 (MCZ).

***Aleiodes (Eucystomastax) lucidus*
(Szépligeti), new combination.**

Macrostomion lucidus Szépligeti, 1906: 609. Holotype male, Bolivia, Mapiro (TMB, #1658) [examined].

Diagnosis.—Body color black, except pronotum laterally and mesothorax orange; BL 8.50–9.33 mm; FWL 8.67–8.70 mm; flagellum with 63F (missing beyond F31 in holotype); MS/EH 0.16–0.31;

TW/EW 0.35–0.75; occipital carina weak ventrally, not meeting hypostomal carina; OS/MS 2.15–2.31; OOD/OD 1.0–1.30; face rugopunctate; temple smooth; maxillary palpus swollen, especially segments 2–4; propleuron smooth; notauli absent; epicnemial carina weak, especially dorsally, or entirely absent; sternaulus absent; propodeum smooth; median propodeal carina present; metasoma comprising 7 visible terga; T1 length/width 1.11–1.18; T2 length/width 0.75–0.80; T3 length/width 0.43–0.54; T1–T4 smooth with scattered punctations; OL/HBTL unknown (males only); pecten of tarsal claw pectinate with 8–9 spines; HTS/HBTL 0.29–0.33; hind coxa dorsally punctate; R1/R2 0.49–0.50; R1/recurrent vein 0.55–0.60; nervulus placement beyond basal vein / nervulus length 1.39–1.50; basella/mediella 0.66–0.83.

Distribution.—Bolivia.

Other Specimens Examined.—Bolivia: 1 male, Santa Cruz, J. Steinbach (MCZ).

Comments.—This species is the rarest of all *Eucystomastax* in collections, and known only from the male. In appearance it is quite similar to *Aleiodes melanopterus* (Erichson), except that *lucidus* has a larger body size, less extensive bright orange color on the metasoma, and generally smoother sculpture. In *lucidus*, terga 2+3 are mostly smooth and shining (except for scattered punctations), the mesonotum is entirely smooth and lacking notauli, and the epicnemial carina is greatly reduced or entirely absent. Although similar to *melanopterus* in size and color, the unusual sculpturing (especially the complete loss of notauli and reduction of the epicnemial carina) is unusual and suggests that *lucidus* is a distinct species. From the apomorphic color pattern (bright orange mesosoma and black metasoma) it might be inferred that *lucidus* and *melanopterus* are sister-species.

***Aleiodes (Eucystomastax) melanopterus*
(Erichson), new combination
(Figs. 1–7)**

Rogas melanopterus Erichson, 1848: 588. Holotype female, British Guiana, Schomburgk (ZMHB) [examined].

Macrostomion peruvianum Szépligeti, 1904: 193. Holotype male, Peru, Marcapata (TMB, #1657) [examined]. NEW SYNONYM.

Rhogas rufithorax Cameron, 1911: 313. Holotype male, British Guiana (BMNH, #3c232) [examined]. NEW SYNONYM.

Rhogas fortipalpus Cameron, 1911: 314. Holotype female, British Guiana (BMNH, #3c234) [examined]. NEW SYNONYM.

Rhogas forticarinatus Cameron, 1911: 314. Holotype female, British Guiana (BMNH, #3c234) [examined]. NEW SYNONYM.

Eucystomastax bicolor Brues, 1912: 223. Holotype male, Brazil, Para, W.M. Mann (MCZ, #29924) [examined]. NEW SYNONYM.

Diagnosis.—Body color as in Fig. 1: head, most of legs apically, and mesosoma apically, all black; mesosoma mostly bright orange; coxae, propodeum, and T1-6 varying from bright orange to black; BL 6.75-8.50 mm; FWL 5.50-7.25 mm; flagellum with 50-56F (males) 56-68F (females); MS/EH 0.17-0.22; TW/EW 0.44-0.59; occipital carina meeting hypostomal carina; OS/MS 2.40-4.0; OOD/OD 1.25-1.50; face smooth; maxillary palpus swollen, especially segments 2, 3, and 4; propleuron smooth; mesonotum smooth, posteromedially with short carina; notaulus smooth; sternaulus smooth; epicnemial carina complete; propodeum smooth dorsally, carinate-rugose basally; T1 length/width 0.91-1.11; T2 length/width 0.70-0.73; T3 length/width 0.43-0.49; T1 rugo-striate; T2 rugo-striate; T3 rugo-striate from extreme base up to entire basal 1/2, otherwise smooth; T4 smooth; OL/HBTL 0.22-0.96; pectin of tarsal claw with 4-9 spines; HTS/HBTL 0.29-0.35; hind coxa dorsally smooth; R1/R2 0.37-0.40; R1/recurrent vein 0.39-0.56; nervulus position beyond basal vein/nervulus length 1.56-2.22; basella/mediella 0.57-0.85.

Distribution.—Widely distributed and relatively common throughout the Amazonian basin of South America from Suriname south to northern Argentina, west to eastern Peru. Not recorded east of the Andean Cordillera or in Central America. Seasonal occurrence from 5 September through 10 May, with collecting records from each intervening month.

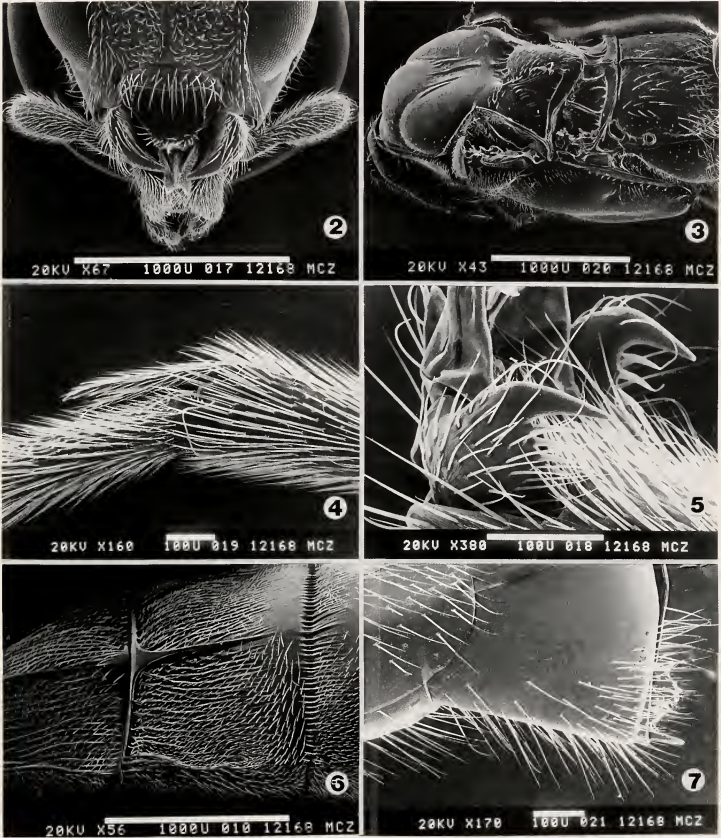
Other Specimens Examined.—(94 females and 310 males) from the following localities. **Argentina:** Jujuy: Alto la Vina, Posta Lozano; Salta: Abra Grande, nr. Aguas Blancas, 24 km NW Aguas Blancas, Camp. Jakulica, Oran, nr. Pocitos, Rio Pescado (Est. YPF), Tartagal, nr. Vespucio; Tucuman: El Nogalar, Horco Molle, Las Cejas, Quebrada Lules, S. Pedro Colalao, Tacunas, Trancas, (C. Porter, E. Willinck, Arnau) (CNC, MCZ). **Bolivia:** Chapare, El Palmar, 100 km N. Bermejo, Chulomani, La Paz, Mapiri, Santa Cruz (A. Garcia, C. Porter, J. Steinbach, L. Pena) (CNC, MCZ). **Brazil:** Goiás, Goiânia; Mato Grosso, Burtiti; Nova Teutônia: Santa Catarina; São Paulo: São Paulo (E. Munroe, C. Porter, F. Plaumann) (CNC, MCZ, FUG). **Ecuador:** Napo, Tena; Pompeya (L. Huggert, Pena, M. Sharkey, L. Masner) (CNC, MCZ). **Paraguay:** Molinascue, Villarica (F. Schade) (MCZ). **Peru:** Cuzco Dep.: Quincemil; Madre de Dios: Tingo Maria; Junin, Satipo (A. Garcia, L. Pena, C. Porter, L. Huggert) (CNC, MCZ).

Comments.—Although the body coloration varies considerably, the basic pattern for the species is quite distinctive: mesosoma mostly orange, and head, wings, legs, and metasoma, at least apically, black. The most notable variation occurs on the pronotum, coxae, trochanters, metathorax, propodeum, and metasomal terga 1-5 which vary from entirely orange to entirely black. Although the metasoma is commonly entirely black, sometimes terga 1-3, and more rarely terga 4-5, are orange or orange irregularly infused with black. This is the most commonly collected *Eucystomastax* species.

***Aleiodes (Eucystomastax) mexicanus* Cresson**

Aleiodes mexicanus Cresson, 1869: 378. Holotype female, Mexico (Prof. Sumichrast) (ANSP, #1658) [examined].

Diagnosis.—Head, antenna, legs, and pronotum black; mesosoma otherwise and metasoma yellowish orange; BL 7.0-8.50 mm; FWL 6.5-8.0 mm; flagellum with 56-62F; MS/EH 0.12-0.15; TW/EW 0.53-0.75; occipital carina weak ventrally, not meeting hypostomal carina; OS/MS 3.50-4.33;



Figs. 2-7. *Aleiodes melanopterus* (Erichson): 2, lower portion of head of female, anterior view showing large oral space and swollen maxillary palpus; 3, mesosoma of female, dorso-lateral view showing predominantly smooth sculpture of mesonotum, mesopleuron, and propodeum (note median carinae of mesonotum and propodeum); 4, hind leg of female, lateral view showing apex of tibia, tibial spurs, and base of basitarsus; 5, hind tarsal claws of female, lateral view showing basal pectination; 6, metasoma of female, dorso-lateral view showing microsculpture of tergum 1, tergum 2, and base of tergum 3; 7, apex of metasoma of female, lateral view showing hypopygium and short ovipositor.

OOD/OD 0.70-0.91; face rugose; maxillary palpus swollen, especially segments 2 and 3; propleuron rugose, except smooth laterally; notaulus scrobiculate; sternaulus smooth; epicnemial carina complete; propodeum rugose; T1 length/width 1.14-1.17; T2 length/width 0.69-0.82; T3 length/width 0.40-0.50; T1 longitudinally aciculate; T2 longitudinally aciculate; T3 longitudinally aciculate basally, apical 1/2 smooth; T4 smooth; median carina present on T1-T2; OL/HBTL 0.18-0.60; pectin of tarsal claw with 8 spines; HTS/HBTL 0.30-0.35; hind coxa dorsally smooth; R1/R2 0.37-0.44; R1/recurrent vein 0.39-0.50; nervulus placement beyond basal vein/nervulus length 2.0-2.67; basella/mediella 0.67-0.73.

Distribution.— Mexico. The one record from Mississippi needs confirmation. This could be an accidental introduction and the species may not be established.

Other Specimens Examined.— **Mexico:** 1 female, Orizaba, 25.vii.1956, R. & K. Dreisbach (USNM); 1 female, Ver., Santecomapan, 10 June 1969, J. E. H. Martin (CNC); 1 female, Sin., 27 mi. E. Villa Union, 26 July 1964, H. F. Howden (CNC); 32 mi. W. San Cristobal, Jct. Hwy. 190-195, Chis., at light, 11 June 1969, A. Mutuuru (CNC). **USA:** 1 male, Mississippi, Lafayette Co., May-June 1960, F. M. Hall (CNC).

Comments.— A relatively rare species in collections, that is similar to both the Neotropical species *A. melanopterus* (Erichson) and the Nearctic species *A. politiceps* (Gahan). However, the metasoma of *melanopterus* (Erichson) is black, at least apically, while the body of *politiceps* is entirely orange. In this regard *mexicanus* is intermediate between *melanopterus* and *politiceps*, but the differences are discrete. One distinctive feature of *mexicanus* is the very narrow malar space, as indicated by the MS/EH: 0.12-0.15 (the lowest malar space/eye height ratio for any member of the species-group). Also, the first metasomal tergite (T1) is somewhat longer and narrower than in other members of *Eucystomastax*.

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which this study was based:

- ANSP The Academy of Natural Sciences, Philadelphia, Pennsylvania (D. Azuma)
- BMNH The Natural History Museum, London (T. Huddleston)
- CNC Canadian National Collection, Ottawa (M. Sharkey)
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (J.M. Carpenter)
- ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin (F. Koch)
- TMB Természettudományi Múzeum Allattara (=Hungarian Natural History Museum), Budapest (J. Papp)
- USNM U.S. National Museum of Natural History, Washington, D.C. (P.M. Marsh)

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The Evolutionary Ecology of Symbiotic Ant - Plant Relationships

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Abstract.—A tabular survey of ant-plant symbioses worldwide summarizes aspects of the evolutionary ecology of these associations. Remarkable similarities between ant-plant symbioses in disjunct tropical regions result from convergent and parallel evolution of similarly preadapted ants and plants. Competition among ants has driven evolutionary specialization in plant-ants and is the principal factor accounting for parallelism and convergence. As habitat specialization accompanied the evolutionary radiation of many myrmecophytes, frequent host shifts and de novo colonizations by habitat-specific ants both inhibited species-specific coevolution and co-cladogenesis, and magnified the diversity of mutualistic partners.

The comparatively high species diversity of neotropical plant-ants and myrmecophytes probably results from two historical factors. Most importantly, influenced by Andean orogeny, greater habitat disturbance by fluvial systems has created a mosaic of habitat types unparalleled in other tropical regions; both myrmecophytes and plant-ants have diversified across habitat boundaries. Second, the arrival of a new wave of dominant ants (especially *Crematogaster*) may have condensed the diversity of relatively timid plant-ants to a greater degree in Africa and Asia than in the more isolated Neotropics. Regular trajectories in the evolutionary histories of plant-ants appear to be driven principally by competition, in a manner analogous to the taxon cycles or pulses proposed for other groups.

"In all the plants I have seen bearing sacs on the leaves, to whatever order they belong, it is remarkable that the pubescence consists of long hairs having a tubercular base; and although I do not see what connection that peculiarity can have with the ants' choice of a habitation, it is probable they find some advantage in it." "Ants' nests in swellings of the branches are found chiefly in soft-wooded trees of humble growth, which have verticillate or quasi-verticillate branches and leaves, and especially where the branches put forth at the extremity a whorl or fascicle of three or more ramuli; then, either at each leaf-node or at least at the apex of the penultimate (and sometimes of the ultimate) branches, will probably be found an ant-house, in the shape of a hollow swelling of the branch..." (Spruce 1908).

INTRODUCTION

A synthetic overview of the evolutionary ecology of mutualism has been disappointingly slow to develop (Bronstein 1991). In large part, this shortcoming may reflect the composite nature of mutualisms, which often arise as parasitisms (Thompson 1982), and frequently convey benefits contingent on physical environments, population densities, and third or multi-species interactions (reviewed in Howe 1984, Addicott 1985, Law and Koptur 1986, Schemske and Horvitz 1988, Thompson 1988, Cushman and Addicott 1991). The lack of a conceptual organization for such complex and variable associations inhibits a search for patterns

in historical and ecological factors shaping the evolution of mutualism. Complicating this endeavor still further is that most studies of mutualism focus on pollination and dispersal systems, which account for 80 % of the articles on mutualism in Bronstein's (1991) survey. Despite excellent treatments available for taxonomically and/or geographically restricted suites of such interactions (e.g., Heithaus et al. 1975, Feinsinger and Colwell 1978, Janson 1983, Herrera 1984, Gautier-Hion et al. 1985, Moermond and Denslow 1985, Gottsberger 1990, Bronstein 1992), both the overwhelming numbers and the taxonomic and ecological diversity of these interactions magnify the difficulty of

identifying single or few organizing processes or principles.

Symbiotic associations between ants and myrmecophytic plants offer a useful counterpoint. Sufficiently small in number to be summarized in a single table (Appendix 1), they nevertheless occur in numbers adequate to provide fertile substrate for hypothesis testing. Their presence in tropical regions throughout the world facilitates comparisons among taxonomic and ecological equivalents evolved in isolation on different continents (McKey and Davidson, in press). Despite their considerable diversity and widespread distribution, these relationships are relatively uniform in structure. Thus all myrmecophytic plants provide permanent housing and food to ants which are known or (more often) presumed to protect their hosts from herbivory or competition, or to provision them with nutrients (reviewed recently in Beattie 1985, Huxley 1986, Jolivet 1986, Hölldobler and Wilson 1990).

Here we provide an overview of the symbiotic ant-plant relationships, focusing principally on trees, shrubs and hemiepiphytes of the American and African tropics. (The epiphytic ant-plants have been reviewed recently elsewhere by Davidson and Epstein 1989.) This geographic specialization reflects our comparatively poor understanding of ant-plant relationships in the Oriental and Australian tropics where, with the exception of ant-epiphytes (Jebb 1985, Huxley and Jebb 1991), investigations are fewer in number and less detailed (but see the recent proliferation of work by Fiala and Maschwitz 1990 and 1991, Fiala et al. 1989 and 1991, Maschwitz et al. 1989 and 1991). For myrmecophytes overall, existing evidence is often too meagre for a convincing assessment of the fitness consequences of particular associations. We therefore avoid using the terms "mutualism" and "facilitation" in favor of less restrictive words like "association", "interaction", or "relationship". For similar reasons, the terms "myrmecophyte", "myrmecophytic" and "ant-plant" are used here only to describe plants regularly inhabited by ants, without implying that plants either benefit from the ants or possess traits evolved principally as ant attractants. On occasion, we also refer to "myrmecophilic" plants, those which are not symbiotic with ants but produce obvious ant attractants

such as extrafloral nectaries (EFN's) and/or pearl bodies.

Our principal themes here are the factors which have predisposed particular ants and plants toward symbiotic association, and the ecological forces which have driven evolutionary specialization in each of these taxa. We also summarize the processes generating and maintaining diversity within each of these groups, as well as the factors limiting species specificity and co-cladogenesis. Finally, we speculate about particular evolutionary trajectories which appear to have occurred regularly across independent lineages of plant-ants and ant-plants. As a prelude to all the above, we briefly review the way in which historical context appears to have influenced the evolution of ant-plant symbioses in the American and African tropics.

DIVERSITY, BIOGEOGRAPHY AND HISTORY

Both plant-ants and myrmecophytes achieve their greatest richness in the American tropics (McKey and Davidson, in press). Among ants, the proportion of neotropical and African genera containing specialized plant-ants is approximately the same, whether calculated by biogeographic region (respectively, 10 % and 12 % of genera) or for mesic tropical environments (12.8 % and 14.5 %, respectively). Although the mesic Neotropics hold approximately 1.3 times as many ant genera as does mesic tropical Africa (Brown 1973), the latter land mass has slightly more genera which contain at least one plant-ant. Nevertheless, two of these genera are monotypic and, based on present knowledge, the species richness of plant-ants appears to be about 3.5-fold greater in the Neotropics than in Africa (current estimates of 85 species versus 24, including one species in Madagascar). Differences in diversity occur principally due to the proliferation of plant-ant species within endemic neotropical genera. In the New World, significant radiations of plant-ants occur in endemic *Pseudomyrmex* (N = 32 species), *Azteca* (N probably > 20), *Myrmelachista* (N > 6), and *Allomerus* (N = 8), as well as in cosmopolitan *Pheidole* (N = 6) and *Pachycondyla* (N = 4). In contrast, significant radiations of African plant-ants are limited to *Tetraponera* (N = 5) and *Technomyrmex* (N = 6),

both widely distributed in the Old World tropics, and even these radiations are comparatively small.

Relative to the ant faunas of both the American and African tropics, those of the Oriental and Australian regions appear to be poor in plant-ant genera (McKey and Davidson, in press); respectively, only 5.6 % and 7.3 % of regional ant genera, and 7.3 % and 9.1 % of mesic tropical genera, contain plant-ants. Moderate to large radiations of plant-ants in the Oriental region include only cosmopolitan *Crematogaster* (N 8 species) and *Camponotus* (N 7), as well as endemic *Cladomyrma* (N 5), and current estimates of plant-ants are only 24 species overall. In the Australian region, encompassing northern Australia, New Guinea and associated islands, such radiations are limited to endemic *Anonychomyrma* (probably > 3 species), and the species richness of plant-ants presently stands now at only about 12 species. Although the numbers of plant-ants may increase slightly in these regions due to increased sampling effort (cf. Dorow and Maschwitz 1990, Maschwitz et al. 1991) and taxonomic revision (e.g., S. Shattuck, 1991, 1992b), the relative poverty of plant-ants at the generic level is likely real.

Myrmecophytes probably constitute a similar fraction of all plant genera in the American and African tropics, but their species richness is distinctly greater in the Neotropics (McKey and Davidson, in press). Again unmatched in Africa, major radiations of ant-plants within (mainly) endemic, neotropical genera largely account for this difference. Neotropical plant genera with significant radiations of myrmecophytes include endemic *Cecropia* (N 50-60 ant-plant species), *Tachigali* (N 20), *Triplaris* (N = 17), *Tococa* (N = 40-45), *Clidemia* (N = 15-20) and *Maieta* (N 15), as well as non-endemic *Acacia* (N 12 species), *Ocotea* (N 6) and *Hirtella* (N = 6). In contrast, in Africa only *Acacia* (N 15) and, to a lesser extent, *Cuviera* (N = 8+), *Canthium* (N = 3-6) and *Clerodendrum* (N 3) contain moderate to large numbers of ant-plants, and of these genera only *Cuviera* is restricted to the Ethiopian region. Estimates of myrmecophyte species richness are about three-fold greater in the American than the African tropics, and maximum local (alpha) diversity may be twice as high. Although it is not yet possible to

estimate the frequency of myrmecophytes in the tropical floras of Oriental and Australian regions, substantial radiations of myrmecophytes within genera are comparatively limited (references in McKey and Davidson [in press]). These probably include only *Macaranga* (N 23), *Korthalsia* (N = 7+) and *Neonauclea* (N = 4+) in the Oriental tropics, and *Chisocheton* (N = 6), *Kibara*, *Stegantnera*, and *Semecarpus* (each with N = 4) in the Australian tropics. Altogether, the Oriental and Australian tropics likely hold slightly more than 100 myrmecophyte species.

At the generic level, the determinants of ant-plant and plant-ant diversity in the American and African tropics are probably similar to those regulating species richness of the floras and ant faunas overall (McKey and Davidson, in press). Radiations of myrmecophytes and plant-ants in both areas appear to have been strongly affected by both the climatic and geologic histories of the continents and to have been correlated with diversification in habitat use. As may be common for neotropical plants in general (Gentry 1986, 1989 and in press, but see Simpson and Todzia [1990] for the high Andean flora), generic radiations of ant-plants may often be comprised of neoendemics with comparatively recent origins. Frequently geographically or edaphically restricted, such species may be products of a "species pump", postulated to have generated new species through habitat specialization during range reexpansions within interglacial intervals of the Pleistocene (Colinvaux, in press). Although the diversity of tropical ant species has not previously been related explicitly to any similar mechanism, a possible link between speciation and habitat specialization is evidenced by the observation that many plant-ants show greater specificity to habitats than to host species (Benson 1985, Davidson et al. 1989 and 1991; Longino 1989a and 1991a).

Given historical and contemporary differences in geological activity, and in correlated rates of habitat disturbance on the two continents, the American tropics should have provided greater opportunity than did tropical Africa for habitat specialization and speciation (McKey and Davidson, in press). Topographically, the mesic African tropics occupy a comparatively flat and featureless plain, much

more homogeneous than mesic tropical America. In the Neotropics, orogenic activity in the Andes has not only influenced the montane and submontane areas directly, but has given rise to the fluvial disturbances that helped to create a spectacular mosaic of landscapes over the vast Amazonian region. No less than 26 % of modern lowland forests of Western Amazonia give evidence of recent erosional and depositional activity, and approximately 12 % of these lands are currently in some stage of succession (Salo et al. 1986, Räsänen et al. 1987). In addition to their role in creating and maintaining a landscape mosaic conducive to rapid speciation, the Andes also appear to have protected the mesic Neotropics from the severe and frequent droughts which could have magnified species extinctions in Africa, as mesic forests were repeatedly reduced and fragmented during Pleistocene times (Raven and Axelrod 1974, Axelrod and Raven 1978).

Finally, neotropical species should also have received greater protection than their African counterparts from Pleistocene temperature variation. Lowland Africa is approximately 500m higher in elevation than is lowland Amazonia, and would have provided fewer refugia for plants and animals during glacial periods. Current evidence (e.g., Bengo and Maley [1991]) indicates that montane forest, including elements now restricted to the cool, moist conditions of the Afromontane zone, extended to low elevations (600 m or perhaps lower) in Central Africa during several periods over the last 135,000 years. Judging from the dramatic drop in ant diversity and abundance with elevation on humid tropical mountains (Janzen 1973), the conditions suggested for these periods would not have been conducive to the success of much of the contemporary ant fauna of lowland African forests. To the extent that climatic fluctuations in Africa exceeded those in the American tropics, these could have led to the dissolution of mutualisms, even without species extinctions, as the fitness consequences of association shifted (e.g., to parasitism) with fluctuations in the abiotic and biotic environments.

SIMILARITIES BETWEEN ANT-PLANT RELATIONSHIPS OF DIFFERENT TROPICAL REGIONS

In the context of the aforementioned differences in species richness, and in the climatic and geologic histories of ant-plants on different tropical land masses, certain similarities in the form and ecology of ant-plant relationships of different continents appear all the more striking. For example, across tropical land masses, large colonies of active and aggressive ants occupy fast-growing and light-demanding pioneer trees (neotropical *Cecropia* and Old World *Macaranga*). In contrast, timid ants inhabit small, slow-growing understory shrubs or treelets with hairy domatia (e.g., American *Hirtella*, *Duroia*, and many melastomes, and African *Magnistipula*, *Delpydera*, *Cola*, and *Scaphopetalum*). Finally, myrmecophytic trees of secondary forests and forest light gaps (neotropical *Triplaris* and African *Barteria*) grow in circular clearings made by pseudomyrmecine ants, which attack vegetation in the neighborhood of their hosts. McKey and Davidson (in press) have amassed evidence against common ancestry as a general explanation for these remarkable commonalities. While some comparisons between Africa and Asia suggest common descent of ant-plants, plant-ants or both, myrmecophytes and specialized plant-ants appear to have evolved largely independently in America and Africa. No ant-plants of Africa and the Neotropics have apparently shared a myrmecophytic common ancestor. In contrast, the plant-ant habit may be ancient in the sub-family Pseudomyrmecinae and in tribes Myrmelachistini and Tapinomini, and might possibly have preceded the splitting of South America and Africa. However, with these possible exceptions, resemblances between symbiotic associations in the American and African tropics are not due to common descent of one or both partners from an association that predated continental separation or other vicariance events, or which migrated intact from one continent to the other (McKey and Davidson, in press).

The remarkable correspondences between ant-plant associations in the American and African tropics must therefore be due to some combination of: (1) parallel evolution of ants and/or plants from

similar starting material, (2) evolutionary convergence, and (3) the matching of symbiotic partners according to a set of shared rules. The task then is to identify the preadaptations which have been pressed into service and evolutionarily modified in symbiotic ants and plants, and to recognize the selection pressures which have led repeatedly to the correspondences noted above.

PREADAPTATIONS OF PLANTS AND ANTS

Parallel and convergent evolution are usually regarded as evidence that selection pressures have acted in similar ways on organisms of different lineages. Selection, however, is only part of the explanation for these phenomena. Different lineages may follow similar evolutionary trajectories because they share similar developmental constraints which channel the action of selection along a limited number of paths.

Preadaptations for Myrmecophytism

The evolutionary antecedents of specialized myrmecophytic traits are poorly explored. However, comparative studies of myrmecophytes and their less specialized relatives are beginning to suggest plausible and testable hypotheses about the origins of these traits (Benson 1985, McKey 1989 and 1991, O'Dowd and Willson 1989, Fiala and Maschwitz 1991, Schupp and Feener 1991). For example, in various plant taxa, a few similar structures have repeatedly provided the raw materials transformed by selection into myrmecophytic structures. An understanding of the origins of these traits may help to identify constraints which have pressed ant-plants of diverse lineages and biogeographic regions into a limited number of molds. It may also indicate developmental patterns which have facilitated the evolution of myrmecophytism, and suggest why myrmecophytes have evolved repeatedly in some lineages, but rarely or never in others.

Provision of Food for Plants.—Discussion of the evolutionary background of myrmecophytes has tended to emphasize the provision of food for ants. Indeed, there is evidence from many lineages that the ancestors of ant-plants possessed extrafloral

nectaries, pearl bodies, or other traits, which provided food for ants in loose non-symbiotic interactions. The large, complex nectary glands of some ant-plants (e.g., *Acacia*, *Endospermum*, and some *Macaranga*), and the elaborate food bodies of others (e.g., Müllerian bodies of *Cecropia*, and Beccarian bodies of Asian *Macaranga*) are readily accounted for as outgrowths of these traits. As ant-plant interactions intensified into symbiosis, such attributes should have been easily modified by selection acting on the composition and rate of supply of food for ants. The Beltian bodies of Central American ant-acacias may be the only case in which a specialized food-producing structure of a myrmecophyte lacks an obvious antecedent among unspecialized but related plants.

Provision of food ensures that ants are a regular component of the plant's biotic environment, and doubtless facilitates the evolution of more intense interactions. However, myrmecophytes have evolved in only a small subset of the numerous plant lineages whose members are engaged in opportunistic myrmecophilic interactions; other plant traits must also play a role in facilitating or constraining the evolution of symbiotic interactions. Furthermore, in many cases, neither the myrmecophytes nor their close relatives provide food directly to ants. In many cases, EFN's and food bodies are lacking, and scale insects (Coccoidea, Homoptera) are a major source of colony nutrition (Appendix 1). Following Ward (1991), we suggest that many myrmecophytic relationships evolved not from pre-existing myrmecophilic relations, but from parasitisms in which stem-nesting ants began to inhabit live plant cavities and to tend Coccoidea.

Structures for Housing Ants.—We must thus explore plant traits that facilitated the production of cavities that could be modified by selection into specialized structures for housing ants. The evolutionary antecedents of myrmecodomatia, the defining feature of specialized myrmecophytes, have received little attention. Preadaptations and developmental constraints in the evolution of myrmecodomatia will be discussed in detail elsewhere (McKey, in preparation) and are summarized only briefly here.

Table 1 Taxa in which at least some myrmecophytes have long, dense hairs which inhibit insect movements on stems, domatia or both.

Region	Family	Genus
ETHIOPIAN	Chrysobalanaceae	<i>Magnistipula</i>
	Dichapetalaceae	<i>Dichapetalum</i>
	Ebenaceae	<i>Diospyros</i>
	Rubiaceae	<i>Canthium</i>
		<i>Cuviera</i>
	Sapotaceae	<i>Delpyodora</i>
	Sterculiaceae	<i>Cola</i>
		<i>Scaphopetalum</i>
NEOTROPICAL	Boraginaceae	<i>Cordia</i>
	Chrysobalanaceae	<i>Hirtella</i>
	Fabaceae	<i>Platymiscium</i>
		<i>Tachigali</i> ¹
	Gesneriaceae	<i>Besleria</i>
	Melastomataceae	<i>Allomaiaeta</i> ²
		<i>Blakea</i> ³
		<i>Clidemia</i> ⁴
		<i>Conostegia</i>
		<i>Henriettea</i> ⁵
		<i>Maieta</i>
		<i>Sagraea</i> ⁶
		<i>Tococa</i> ⁷
	Cecropiaceae	<i>Pouroma</i>
	Polygonaceae	<i>Triplaris</i>
	Rubiaceae	<i>Duroia</i> ⁸
		<i>Hoffmannia</i>
		<i>Remijia</i>
ORIENTAL	Melastomataceae	<i>Medinilla</i>
	Verbenaceae	<i>Callicarpa</i>
	Piperaceae	<i>Piper</i>
AUSTRALIAN		
	Monimiaceae	<i>Steganthera</i>

¹ At least one species, collected from a hillside over the junction of the Rio Sotileja and the Rio Manu, in southeastern Peru (D. Davidson, unpublished).

² Closely related to *Maieta* (A. Gentry, personal communication)

³ Benson (1985) considers the leaf pouches of *B. formicaria* to be in transition from acarodomatia to ant-domatia. Among the melastomes listed here, *Blakea* is unique in not belonging to the Miconieae.

⁴ At least three independent origins of domatia in *Clidemia* sensu strictu; includes *Myrmidone* (Judd and Slean 1991)

⁵ Includes *Henriettella* (Judd 1989)

⁶ Includes *Ossaea* p.p. (Judd 1989)

⁷ Includes *Microphysca* (Judd and Slean 1991)

⁸ Two independent origins of domatia (foliar domatia and swollen internodes)



Fig. 1. Paired leaf-pouch domatia, covered with dense, erect trichomes, at the base of a leaf of *Delpyhora macrophylla* Pierre (Sapotaceae) in southern Cameroon. These pouches are formed by downward folding and rolling of the expanded base of the blade on either side of the midrib. The domatia are usually occupied by timid *Technomyrmex* species.

Stipules have been modified into ant-domatia in a few myrmecophytes; known examples are all from the Old World tropics (Appendix 1). (The only apparent exception is *Acacia*, in which thorns, themselves highly specialized stipules, have been modified into domatia in both neotropical and Old-World representatives.) In many tropical plants, large stipules function as mechanical protection for the growing bud. In some cases, stipules possess ant-attractive structures which provide biotic defense as well. Where stipules are persistent, rather than being shed soon after maturation of associated nodes, ants may find suitable shelter for tending homopterans, nesting, or both. Although ants and their associated debris are observed frequently beneath large stipules, only rarely have these stipules become evolutionarily modified to house ants. Specializations include recurving or inflating of the

stipule to form a more enclosed structure (as in New Guinea *Psychotria* and perhaps African *Dactyloadenia*), location of specialized food bodies on the lower surface of the stipule (Asian *Macaranga*), and possibly the evolution of persistent stipules. In an analogous case, African *Diospyros conocarpa* Gürke & K. Schumann has specialized, hairy domatia formed from persistent cataphylls (Letouzey and White 1970). These structures are leaf-like appendages, usually rapidly deciduous, and formed on the first few nodes of young expanding twigs in many tropical trees with rhythmic growth patterns (Hallé et al. 1978). They are functionally analogous to stipules. In *D. conocarpa*, the cataphylls are folded to form a structure completely enclosed, except for a small opening near the base of the blade, and they are persistent, rather than deciduous, as in related species. These structures

are occupied by *Technomyrmex kohlitzii* (Forel), which also inhabits several leaf-pouch ant-plants in the same forests.

In Asia, Africa, and the Neotropics, leaf-pouch domatia of strikingly similar form have evolved in numerous myrmecophyte lineages (Appendix 1). Formed near the leaf base, and typically paired on either side of the midrib (but single in some species), they are usually covered with long, dense trichomes (Table 1). Restricted to understory treelets and shrubs, these ant-plants typically are occupied by small, timid ants. Leaf-pouches seem to be formed in one of two ways. In some taxa (e.g., neotropical Melastomataceae, and African Sterculiaceae), invagination occurs in the internal portion of the leaf blade, in a region flanking the base of the midrib. This invagination produces single or paired inflated pouches, each with an entrance on the abaxial leaf surface. In at least four plant families, including most frequently and variably in the Rubiaceae, paired leaf pouches form in a different manner. At the bases of leaf blades, (revolute) leaf margins curl downward, as in African *Delpyodora* (Fig. 1), *Magnistipula*, *Dichapetalum gassitae* Bret., and *Ixora hippoporifera* Bremek., neotropical *Hirtella* and *Remijia*, and Asian *Callicarpa saccata* Steen. Less frequently, (involute) leaf margins curl upward, as in neotropical *Duroia saccifera* Benth. and Hook. Pouches may be bubble-like invaginations (*Gardenia imperialis* L. Pauwels) or, more often, scroll-like hollow tubes.

It has long been postulated that the leaf-pouch domatia of ant-plants evolved from acarodomatia (Schnell 1966, Schnell et al. 1968), presumably by intermediate stages in which domatia could be occupied either by mites or by small ants. Selection led to increased size of domatia with progressive transference of protective function from mites to ants (O'Dowd and Willson 1989). Benson (1985) also argues that leaf-pouch domatia evolved in myrmecophytes from small depressions in leaf surfaces. The original function of these depressions was to shelter ant-tended homopterans. The two hypotheses are not mutually exclusive, as ants may also have used acarodomatia to shelter homopterans (Benson 1985). Hypotheses implicating acarodomatia in the origin of leaf-pouch ant-domatia receive strong support from cases like

Cola marsupium K. Schumann, in which a single leaf presents a graded series of domatia increasing in size from typical acarodomatia at the leaf apex to large inflated pouches at the leaf base (Schnell and Beaufort 1966).

Why have leaf-pouch domatia evolved repeatedly in certain groups, for example, at least nine times in the tribe Miconieae in the Melastomataceae (Table 1)? Leaves of many Miconieae have strongly arcuate venation with sections of the leaf blade vaulted and curved upward between major veins. Even before selection intervened to enlarge these structures, this waffle-like leaf organization may have fortuitously provided invaginations large enough to shelter ant nests. In African Sterculiaceae, where similar domatia have evolved twice, venation is also palmate, with three large veins converging at the leaf base.

The largest group of myrmecophytes is that in which domatia are located in stems, or in stem-like structures such as petioles or inflorescence stalks (Appendix 1). Increasing evidence supports the hypothesis that ants originally colonized cavities created in twigs and petioles by wood-boring insects (Ward 1991, also Appendix 1). Together with cavities formed by spontaneous drying of pith canals, these cavities provided ants with shelter and substrate for brood and symbiotic Coccoidea. When the presence of ants conferred net benefit (e.g., by protection against phytophagous insects, including wood-borers, and any diseases transmitted by these insects), selection acted on the plant to evolve features facilitating its occupancy by ants (Ward 1991). Such traits include specialized swollen twigs and a prostoma, or relatively unligified spot through which ants gain easy access to the domatia.

What traits may have predisposed plants to evolve symbiotic association with ants via this mechanism? Wood-boring insects usually attack soft, pithy portions of stems. The larger the primary diameter of a stem, the thicker its pithy central section. Thus thick-twiggged plants offer greater opportunities than do thin-twiggged taxa for wood-boring insects, and for ants which nest secondarily or primarily in the cavities of living plants. Although much poorly understood interspecific variation in stem structure affects the relationship be-

tween the primary diameters and pith diameters of twigs, myrmecophytes are most likely to evolve in plants with thick twigs.

This observation gains importance when we consider the plant-architectural correlates of stem primary diameter. The best known of "Corner's rules," and one confirmed by quantitative studies (White 1983), states that there is a positive correlation between the primary diameter of a stem axis and the size of appendages (e.g., leaves) borne by it (Hallé et al. 1978). This correlation means that selection acting on leaf size (Givnish 1987) also drives evolutionary change in stem diameter (McKey 1991). Thus, the evolution of stem domatia may be facilitated by an evolutionary increase in leaf size, driven for example, by climatic change, by range extension into more mesic environments (Givnish 1987), or by selection to minimize metabolic cost of woody leaf-support tissues (White 1983). If disparities in leaf size were related to habitat, myrmecophyte frequencies could be correlated with habitat, independently of and perhaps even despite any habitat-related differences in selection imposed by symbiotic ants (McKey, unpublished).

Corner's Rule may help account for several groups of ant-plants with domatia in thickened support structures (Appendix 1). First, myrmecophytism has evolved often in genera whose moist, shaded, understory environments have favored comparatively large, broad leaves and thick stems (e.g., African *Leonardoxa*, and Oriental or Australian *Tapeinosperma*, *Steghanthera*, *Kibara*, and *Myristica*). Ants also live symbiotically with members of the Meliaceae, Sapindaceae, and Anacardiaceae, whose leaves are not only large, but compound. In the Meliaceae, myrmecophytes appear to have evolved independently in four genera, including three Asian taxa (*Aphanamixis*, *Chisocheton* and *Aglaia*) with massive stems supporting large compound leaves. Even within *Aphanamixis*, myrmecophily characterizes forms with relatively large leaves and twigs (Mabberley 1985). Second, thick support structures for large leaves may also have facilitated the frequent evolution of ant-plants in fast-growing pioneer trees, whose large leaves and sparse branching allow them to support a considerable leaf surface area

with minimum investment in woody framework (White 1983). Examples are neotropical *Cecropia*, Asian *Macaranga* and Australian *Eudospermum*, which almost surely converged due to selection on leaf size and tree architecture prior to the evolution of myrmecophytism. Other myrmecophytic pioneers of riverine and forest light gaps include neotropical *Triplaris*, Australian *Nauclea* and African *Barteria* and *Vitex grandifolia* Gürke. In all of the plants in these two categories, ant protection might be especially advantageous, because the large and parenchyma-rich meristems are especially susceptible to damage by wood-boring insects. Since most of these plants produce one-to-few large meristems at any one time, the material and opportunity costs of losing even one meristem could be very high.

Finally, two smaller groups of ant-plants house ants in either false nodes, thickened to support multiple leaves (e.g., two *Cordia* species and *Duroia hirsuta* Poepp. and Endl.), or in stout petioles (*Piper*, *Pourouma* and *Tachigali*). Although petioles might often be too short-lived to function as domatia, they are likely to be comparatively long-lived for both the compound leaves of *Tachigali* and the simple leaves of myrmecophytic understory *Piper* species (in which ant cavities also extend into the stem itself).

Preadaptations and Pathways to Specialization in Ants

Specialized plant-ants are represented disproportionately in particular taxonomic categories of ants, and shared characteristics of these taxa provide evidence of factors predisposing ants to evolve symbiotic relationships with plants. Worldwide, plant-ants have evolved in five of 12 subfamilies in the Formicidae (Appendix 1). They are absent only from subfamilies of specialized legionary and other predatory ants (Ceraeopachyinae, Dorylinae, Ecitoninae, Leptanillinae, and Myrmeciinae), and from the monotypic Aneuretinae and Nothomyrmecinae. Until recently, they were also deemed absent from the Ponerinae, the most predatory of five subfamilies containing at least some species that depend directly and substantially on plant resources. However, at least four species of



Fig. 2. Leaves bound together with carton to form the ephemeral nests of *Dolichoderus* (= *Hypoclinea*) *bidens* (L.) in southeastern Peru.

Pachycondyla now appear to be specialized symbionts of *Cecropia* (Davidson et al. 1991, Davidson and Fisher 1991, J. Longino, personal communication). Still, plant-ants are poorly represented in the Ponerinae and among predatory ants in general.

The evolution of obligate plant-ants in five subfamilies, approximately 30 genera (Appendix 1), and multiple clades of at least *Pseudomyrmex* (Ward 1991) and *Azteca* (Benson 1985, Longino 1991a and b) confirms the frequency and facility with which plant-ants have evolved, and provides abundant opportunity to find commonalities in lifestyles and traits that may have promoted evolutionary specialization on plants. For example, three of the six principal generic radiations of South American endemics have arisen (one each) in the sub-family Pseudomyrmecinae, and in the tribes Tapinomini (Dolichoderinae) and Myrmelachistini (Formicinae). These ants share the habit of regularly tending homopterans inside (all three taxa) or outside (especially tapinomines) of cavities in live plants. Within each of these groups, common ancestors of contemporary plant-ants likely had additional traits which predisposed them to evolve symbiotic (parasitic as well as mutualistic) associa-

tions with homoptera and plants. Because the relative competitive abilities of ants form an important part of the story, we turn now to consider various ecological differences among ants with different competitive abilities.

Competitive Dominants.—Ecological limitations on populations of arboreal ants in lowland tropical forests add insight into probable origins, correlates and consequences of arboreal nesting habits, including stem-nesting. Colony populations appear to be limited principally by food and nest sites (Wilson 1959b, Carroll 1979, Davidson and Epstein 1989). Because most arboreal ants are generalized foragers of plant and homopteran exudates, and of carrion, interspecific food requirements are strongly overlapping, and competition can be intense. The competitive dominants of each tropical biogeographic region are species which have evolved means of nesting in areas of abundant food. They include Old World *Oecophylla*, *Crematogaster*, *Tetramorium*, *Philidris* and *Polyrachis*, some Australian *Anonychomyrma*, and New World *Crematogaster*, *Camponotus*, *Azteca* and *Dolichoderus* (including *Hypoclinea*, Shattuck, 1992a). These ants either bind leaves together into

temporary nests, or construct potentially more permanent carton homes in the canopy where food is abundant (Fig. 2). Like species which occupy the top of the competitive hierarchy at high temperate latitudes (Vepsäläinen and Pisarski 1982), these species defend not only their nest sites and temporary, localized food patches, but their entire foraging areas, as absolute territories. Although a certain threshold of aggressiveness may have been required before these ants could defend their somewhat exposed nests successfully against vertebrate enemies (e.g., monkeys and woodpeckers; J. Longino, personal communication), an eventual capacity to nest near abundant food almost certainly contributed to the escalation of aggressive-ness and dominance.

Most competitive dominants tend populations of Homoptera, whose exudates form a steady and predictable source of colony nutrition and help to fund high worker activity and aggression. These ants lack functional stings, but all possess elaborate chemical weaponry (Blum and Hermann 1978, Attygalle and Morgan 1984, Buschinger and Maschwitz 1984, Merlin et al. 1992). Expended in use, these exocrine products should be characterized by more rapid turnover and greater cost than is associated with longer-lived stings and sturdy exoskeletons. Nevertheless, if chemical defenses are supported by the requisite resource base, they appear to be more effective than stings in contests among ants (Davidson et al. 1988). With their rich sources of homopteran exudates, dominants should often experience an excess of dietary carbon in relation to protein, so that colony expansion is protein-limited. If so, this could explain the "high tempo" lifestyle (sensu Oster and Wilson 1978) characteristic of these ants and help to resolve the enigma of their seeming "inefficiency" in foraging (Oster and Wilson 1978; Hölldobler and Wilson 1990). By spending relatively "cheap" carbon resources on aggression and seemingly extravagant levels of activity, these ants secure dominance over territories whose protein resources fund colony growth.

Chemical weaponry and high activity levels are not the only traits determining dominance in these ants. Abundant food and freedom from nest site limitation appear also to have led to larger colony

sizes and longer life expectancies. If the resource environments of ants have helped to shape the evolution of life history attributes (e.g., rates of egg-laying, worker turnover, etc.), a correlated evolved dependency on rapid rates of resource acquisition may restrict some dominants to the most productive sites in lowland rain forests (Davidson and Epstein 1989). Arboreal dominants are preeminent in monopolizing high quality resources at exposed sites such as EFN's, and Homoptera positioned on flowering and fruiting peduncles, where a plant's phloem resources are frequently most concentrated. As evidence of their competitive impact in one rainforest ant community as a whole, Wilson (1959b) noted that a number of arboreal ant species regularly forage on the ground, whereas only a few exceptional ground nesters forage even in the low arboreal zone, and possibly none of these reaches the upper canopy. (In the Neotropics, terrestrially nesting *Paraponera* and *Ectatomma* are obvious counter-examples, but both genera are exceptional among ponerines for their heavy reliance upon plant exudates, carried as large droplets in the mandibles.) Dominants can restrict the local diversity of other ants, as do the parabiotic associates of neotropical ant-gardens (Davidson 1988). Thus, the diversity of arboreal but not terrestrial ant species is lower inside the territories of *Camponotus femoratus* Fab. and *Crematogaster* cf. *limata* parabiotica (Forel), than in adjacent areas lacking these ants. Because the species composition and diversity of subordinate species often varies markedly with the identity of dominants, patchiness in the territories of dominants determines a mosaic of ant communities within many tropical forests (Leston 1973, reviewed in Hölldobler and Wilson 1990).

Competitive dominance may be context dependent, e.g., differing in relation to the identities of plant species which form the substrate for ant nesting and foraging (Davidson and Epstein 1989). Thus, host plant associations of *Oecophylla longinoda* (Latr.) (Dejean and Dijcto 1990) and *Tetramorium aculeatum* (Mayr) (Dejean et al. 1992), two widespread dominants in African forests, are correlated with worker preferences for foliage types offered in laboratory experiments.

Weak Competitors.—For competitively subordinate ants, the benefits of combining nesting and foraging locations are conditional on locating nests and resources in sites which are protected from invasion by dominants. Nests in dead or live twigs, stems, and larval insect borings can be defended if the cavity size is not much larger than the head diameters of workers, soldiers, or queens. By sealing a stem nest with her head, a single worker can protect her whole colony or colony fragment from invasion by enemy ants. Thus, along a Pacific Ocean beach at Corcovado National Park in Costa Rica, the many dead twigs of *Coccoloba* (Polygonaceae) trees were occupied by more than nine ant species (six of *Pseudomyrmex* alone), whose head widths were roughly equal and proportional to the internal diameters of their twig cavities (D. Davidson, personal observation). At least some African *Tetraponera* also appear not to nest in stems whose diameter exceeds a threshold value (Terron 1970). For small-bodied ants like the timid *Wasmannia scrobifera* Kempf in Costa Rica, other protected sites may include carton shelters beneath leaves of plants whose dense stem trichomes exclude larger bodied workers (see below).

For comparatively docile and subordinate ants, the advantage of locating their resources inside stem cavities is clear. The evolutionary transition from nesting in dead twigs to nesting in live twigs and other cavities of live plants conveyed the additional opportunity to obtain uncontested resources from phloem-feeding Homoptera (especially Coccoidea), which either invaded such cavities on their own or were brought there by the ants. Moreover, nests in live wood were potentially habitable over much longer time periods than those in dead or decaying twigs and branches, obviating a need for frequent and dangerous nest moves. Longer tenure of living nest sites, which grew rather than decaying with time, may secondarily have allowed the evolution of larger colony sizes and increased opportunities for local monopolization of resources, as well as the selective advantage of aggressive behavior and allelochemicals. Traits conferring a capacity to nest in live plants are not well studied, but they probably involve evolutionary adjustment to an increased threat from nest pathogens. Thus, Ward (1991) points out the tendency for hypertro-

phy of metapleural glands in domatia-inhabiting pseudomyrmecines. Where studied, the function of metapleural secretions has been tied to the suppression of microbial pathogens (e.g., Maschwitz 1974, Hölldobler and Engel-Siegel 1984).

In summary, plant-ants are most frequent in taxa which depend directly or indirectly, but substantially, on plant resources. They are most likely to have evolved in competitively subordinate ants, selected to live in close proximity to food resources, but to nest and feed in comparatively protected and permanent sites which reduce dangerous contact with competitive dominants. Within this subset of ant taxa, selection for evolutionary specialization of plant-ants might have been less likely in groups where potent defensive exocrine compounds (e.g., many *Dolichoderus* species), and worker armor or specialized diets (e.g., cephalotines) diminished the hazards of encounters with dominants.

The transition from more generalized ancestors to specialized plant-ants would not have been difficult. Founding queens should have evolved greater efficiencies in locating hosts that provided superior food or housing or were more easily accessed. By consuming or deterring insect herbivores, ants might then have enhanced their own fitness indirectly by promoting the vigor or prolonging the lifespans of their hosts. However, host specialization by ants, as well as consumption of eggs and larvae of insect herbivores, could have been favored in ants whether the ants and Homoptera had a net positive or negative effect on these hosts. Longino (1987), for example, discusses the case of *Leptothorax obturator* Wheeler, which nests only in cynipid galls of oaks and probably has no fitness effect on the host tree. Selection pressures on ants and plants should often have been asymmetric, leading to the expectation that ant-attractive traits would have evolved in only a subset of the host plants on which obligate plant-ants reside.

Expectations based on this brief review of competitive interactions among arboreal ant species can now be compared with actual patterns in the distribution and ecology of specialized plant-ants.

THE MATCHING OF ANTS AND PLANTS

Appendix 1 is a worldwide summary of all symbiotic ant-plant relationships known to us. To facilitate comparisons among ants of differing lifestyles and competitive abilities (see below), we organize the data by ant genus. Also evident in this summary is the basic asymmetry in the degree to which relationships are obligate for ants versus plants. The vast majority of the ants in the table are thought to be obligate plant-ants (column 7, though these are not necessarily host-specific). However, a substantial fraction of their host genera have no obvious myrmecophytic traits (column 6), despite their regular association with specialized (usually) or unspecialized ants (cf., African *Musanga* and Neotropical *Tetrathylacium*). Few plants with conspicuous myrmecophytic traits (e.g., obvious domatia, or naturally hollow stems with prostomas) lack specialized plant-ants altogether, though some may occur principally with unspecialized ants in marginal habitats, or at the edges of their distributions (see below).

Almost certainly, Appendix 1 includes a mix of relationships in which ants are parasitic, commensalistic, or mutualistic with their hosts, and the net outcome of the interactions might even vary with habitat or ecological context. These outcomes are not wholly predictable from myrmecophytic traits, since even in mutualistic associations, plants need have no obvious specializations to attract ants. Clearly most of the relationships are poorly known, and many of the table entries are incomplete. Yet the table clarifies the types of data which will eventually be essential to describe pattern in these relationships, and we hope it will stimulate the collection of such data in future studies.

Despite limited data, patterns in relationships of ants and host plants correspond roughly to those noted for tropical forest ant faunas as a whole. Across genera, the fastest growing myrmecophytes of disturbed forest edge (i.e., hosts with rapid rates of resource supply to ants) tend to be inhabited by ants from aggressive, dominant, carton-building genera (column 1), e.g., the *Azteca* of neotropical *Cecropia*, and *Crematogaster* of ecologically similar Old World (especially Asian) *Macaranga*. Less aggressive and competitively subordinate ant spe-

cies tend to persist by employing one or more of several strategies likely to reduce interactions with the dominants. We deal with each of these in turn.

Ant Pruning of Host-plant Neighbors

The most common and significant natural enemies of ants are other ants (Haskins 1939). Species with sting defenses, usually inferior to chemical defenses in contests among ants, are disproportionately likely to attack and prune vegetation surrounding their hosts (Davidson et al. 1988, also column 4, Appendix 1). In both Africa and South America, this behavior is most widespread in pseudomyrmecine plant-ants, where pruning has evolved multiple times in independent lineages (Ward 1990). The potent stings of pseudomyrmecines may be an effective deterrent of vertebrates (Janzen 1972), but they are inferior to chemical defenses in repelling colonies of invading ants. Although the *Pseudomyrmex* of *Triplaris* and *Acacia*, and the *Tetraponera* of *Barteria*, do not forage extensively off their host plants, they regularly leave these hosts to sever the petioles of leaves on neighboring plants (Fig. 3). Eventually these neighbors die, leaving the host trees in starkly defined clearings within the forest.

Such clearings have been hypothesized to reward resident colonies by enhancing host-plant vigor or, in drier environments, acting as natural fire breaks (Janzen 1967a). However, experimental evidence suggests that a more immediate selective advantage for attacks on neighboring vegetation is the reduction of threats from more dominant arboreal ants. When permanent wire bridges were made between myrmecophytic *Triplaris* and neighboring trees, the frequency of invasions by dominant *Crematogaster* increased, and whole hosts or portions of these hosts were eventually usurped by *Crematogaster* or *Azteca* species (Davidson et al. 1988). The broad taxonomic distribution of obligate and facultative pruning behavior (the latter occurring only in the presence of enemy ants, Appendix 1, column 4) suggests that dominant competing and predatory ants constitute a major threat to many or most specialized plant-ants. Its prominence in neotropical ants is evidence against the hypothesis that a paucity of dominants charac-

terizes that region (Carroll 1979, see also McKey and Davidson, in press). Presumably, pruning behavior could also serve to defend resident colonies against invasions by leafcutter (Morawetz et al. 1992) and legionary ants, which could devastate the resource base or the colony itself.

Pruning behavior is not strictly limited to ants with functional stings (Appendix 1). Most neotropical *Cecropia* and Old World *Macaranga* and *Endospermum* establish in disturbed second growth vegetation, where vines are particularly abundant and troublesome to both plants and ants, and where weedy dominant ants are a constant threat (Benson 1985). Not surprisingly, the common ant associates of these host genera (*Azteca*, *Crematogaster* and *Camponotus*, respectively) will attack encircling vines (Appendix 1, Janzen 1969, Fiala et al. 1989; Davidson personal observation, Letourneau et al. 1993), though pruning is not typical for these genera as a whole. The comparatively unbranched growth forms of these hosts may also help to limit contact with vines and neighboring plants (Putz and Holbrook 1988) and, therefore, with enemy ants (Benson 1985). In contrast to chemically defended ants, in which pruning is restricted to species inhabiting hosts of secondary forest, species defended principally by strong or weak stings (*Pachycondyla*, *Tetraponera*, *Pseudomyrmex*, and *Allomerus*) also tend to prune around hosts in primary forests, where threats from vines and dominant ants are not so severe. Not all plant-ants in these genera prune, but some species benefit from other forms of protection (see below).

Worldwide, the most dramatic case of allelopathy by ants may be that of *Myrmelachista* (Formicinae) species inhabiting myrmecophytes in the intriguing western Amazonian "Supaychacras" (Quechua for "Gardens of the Devil"). Dominance of lowland forest stands (to > 10,000 m² in size) by multiple species of myrmecophytes, most prominently *Duroia hirsuta* [Poeppig and Endl.] K. Schum., but also *Cordia nodosa* Lam. and *Miconia nervosa* Triana, suggests that the ants kill non-myrmecophytes selectively (Campbell et al. 1989). In a similar phenomenon, at somewhat higher elevations of western Amazonia (700-1200 m), a different *Myrmelachista* species creates monospecific stands of myrmecophytic *Tococa occidentalis*

Naudin (Morawetz et al. 1992). The two congeneric ants share a similar behavioral ecology (D. Davidson, personal observation, for supaychacras, and Morawetz et al. 1992, for *Tococa*). Workers do not appear to forage off their hosts, but do leave their hosts to attack other plants. When seedlings or saplings of plants other than the host species are placed in the vicinities of these hosts, workers gnaw at the vascular bundles of leaves of the introduced plants, and can kill them in a matter of hours to days. Morawetz and colleagues describe the extraordinary capacity of these ants to single out especially vulnerable plant tissues for attack. Thus, workers bite and poison palmate leaves at the base of laminae, where all vascular bundles join, pinnately nerved leaves at nerve bases of the first and second order, and monocots (e.g., palms), nerve by nerve, along the entire leaf. Necrosis originating at the attack sites spreads rapidly over the entire lamina. Within a few hours to a few days, inhabitants of the *Tococa* can successfully kill seedlings and saplings within a radius of 4 m and damage trees up to 10 m in size. Light gaps created by ant activities are subsequently colonized by vegetative propagation of the host.

Although Morawetz and colleagues discount the hypothesis that the killing of host plant neighbors by *Myrmelachista* has evolved principally to exclude enemy ants, several observations suggest that the hypothesis should not be ruled out. First, leaf-cutter ants, an important enemy of the *Tococa*, invade principally by contact with the branches of other plants, not via the main trunk. Second, no generalized arboricolous ants appear to forage within the territories of these specialized *Myrmelachista*. Furthermore, large worker forces may be needed to assure the safety of ants which have left their hosts. Attacks on neighbors of *Tococa* begin when the ant population of one or a few individual hosts is at least 1500 workers in size. Similarly within supaychacras, smaller fragments of the extended colonies show extreme fidelity to their individual hosts, and only workers of the largest trees leave their hosts to swarm over seedlings and other vegetation. Moreover, the latter activities appear to be restricted to hot and sunny conditions (D. Davidson, personal observation), which may allow maximum worker activity and performance levels. To date,



Fig. 3. *Pseudomyrmex dendroicus* Forel on branches of neighboring plants, whose leaves have been pruned by the ants. The long, thin body shape of workers in *Pseudomyrmex* spp. may preclude their use of plants with long, dense trichomes.

there have been no experimental tests of the effects of creating artificial and unseverable bridges between neighboring intact trees and hosts of these *Myrmelachista*. Such experiments would greatly aid in assessing the evolutionary significance of the extraordinary behavior of these ants.

Hiding among Trichomes

The long, dense and erect trichomes on stems and domatia of many myrmecophytic plants form mechanical barriers to the movements of large-bodied ants and create safe havens for colonies of obligate plant-ants with timid and diminutive workers (Davidson et al. 1989; Fig. 4, Appendix 1). Ant-plants with inhibitory hairs on stems, domatia or both, occur in at least 18 neotropical genera (eight within Melastomataceae alone), and eight families, and appear to have evolved independently on at least 21 separate occasions (Table 1). In Africa, such hairy ant-plants occur in at least eight genera and six families, with each generic occurrence representing a single independent origin. Trichome-

myrmecophytes have also evolved in at least four genera in the Oriental and Australian tropics (Table 1), though the symbiotic associates of these plants remain unknown. In many or most genera of hairy ant-plants, long, erect pubescence also occurs in non-myrmecophytic congeners. It therefore seems likely that docile, small-bodied ants initially sought safe nesting and foraging sites on hairy plants prior to the evolution of myrmecophytism in these lineages. A possible contemporary example of such a relationship is that between *Wasmannia scrobifera* and a non-myrmecophytic hairy *Piper* species in Costa Rica (D. Davidson, personal observation). These ants build small fragile carton nests on abaxial leaf surfaces, where they feed on pearl bodies. Nests are not limited to individual host plants, nor are the ants likely to be obligate plant-ants. In some cases, ant dependency on plant trichomes may be restricted to the early stages of colony foundation. Thus, certain *Azteca* species regularly initiate colonies on pubescent ant-plants like *Cordia* and *Tococa* but later prune runways through host-plant trichomes and form carton satellite nests on neighboring trees lacking protective trichomes ("i" in col-



Fig. 4. Tiny *Pheidole minutula* Mayr workers travel easily among the erect trichomes of this myrmecophytic *Clidemia*. Numerous ant species with tiny workers use such "trichome myrmecophytes" as protected feeding and nesting sites, where they are safe from larger-bodied competitors and predators.

umn 4 of Appendix 1; D. Davidson, personal observation, Benson 1985).

Contemporary distributions of ants across myrmecophytes in Africa and the Neotropics illustrate the influence of plant trichomes on the match between ants and plants (Appendix 1). First, in both regions, worker ants of pubescent myrmecophytes are short-bodied (<3 mm), with short turning radii, and do not include longer-bodied pseudomyrmecines. Included here are two neotropical genera with functional stings (*Allomerus* and *Solenopsis*), and docile African dolichoderines in the genus *Technomyrmex* (species formerly placed in *Engramma*, Shattuck, 1992a). All known hosts of *Allomerus* and *Solenopsis* possess long erect pubescence. *Allomerus* is particularly conspicuous in its association with a diversity of pubescent host genera, seven in total. Of the recorded hosts of African *Technomyrmex*, species in five (and possibly six) of eight genera are hairy; only two, *Leonardoxa* and *Ixora hippoporifera*, definitely lack trichomes. To the extent that members of competitively dominant ant genera depend on pu-

bescent ant-plants beyond the incipient colony stage, the particular species represented in these associations are unusually timid for their genera (e.g., the *Crematogaster* cf. *victima* group on melastomes, the tiny *Crematogaster* sp. on *Delpydera*, and the *Azteca* species inhabiting hairy *Triplaris poeppigiana* Weddell). Second, the body sizes of plant-ants tend to be correlated with trichome spacing (Davidson et al. 1989). This suggests that ancestral ants may have nested preferentially not only on pubescent plants but specifically on those where mean distances between trichomes were no larger than required by their own body sizes. The parallels with nest selection by stem-diameter in generalized stem-nesting ants are obvious (see above).

Third, if ants compete for host plants (see Davidson et al. 1989), and if small, timid species persist only where protected by trichomes from larger dominants (>3 mm, e.g., *Crematogaster* and *Azteca*), then the dominants should prevail on myrmecophytes lacking inhibitory trichomes. This hypothesis is supported not only across ant-plant

genera (Appendix 1), but within several genera which are interspecifically variable in pubescence. In neotropical *Cordia*, for example, glabrous *C. alliodora* (R. and P.) Oken is regularly occupied by aggressive *Azteca*, but smaller and more timid *Allomerus* ants inhabit densely hairy *C. nodosa*. As noted above, a small-bodied and timid *Azteca* species inhabits the hirsute stems of *Triplaris poeppigiana*, though the vast majority of myrmecophytic *Triplaris* species are glabrous and occupied by long and narrow-bodied pseudomyrmecines. Third, dominant *Crematogaster* ants occupy glabrous African *Canthium*, whereas hairy congeneric hosts are associated with timid *Technomyrmex* species (Bequaert 1922, pp. 474-475). The same may perhaps be true in African *Cuviera*, which contains both glabrous and hirsute myrmecophytes. Both *Technomyrmex* and *Crematogaster* are recorded as associates of ant-plants in this genus, but the distribution of different ants in relation to plant pubescence cannot be discerned from existing literature. Finally, as noted above, some ants 3 mm in body length occasionally occupy trichome myrmecophytes but regularly prune trail systems, which facilitate their movements (Davidson et al. 1989).

Association of *Camponotus* ants with spiny palms in the genus *Korthalsia* may also have had its origins in the tendency of ants to feed and nest where the plant's growing tips are protected from the ants' natural enemies. Among the 12 *Korthalsia* species which Dransfield (1984) lists for Sabah, Malaysia, seven have armed ocrea and five do not. Of the species with spiny ocrea, all but *K. ferox* Becc. also show regular associations with ants, whereas this is true for none of the species with unarmed ocrea. Both the long, sharp and comparatively dense spines of species *K. echinometra* Becc., *K. hispida* Becc. and *K. robusta* Blume, and the scattered, short, triangular spines of *K. cheb* Becc., *K. furtadoana* J. Dransf. and *K. rostrata* Blume are more likely to protect the ants from vertebrate predators than from other ants. Dransfield (1981) found greater herbivory by vertebrates (perhaps squirrels) on growing tips of *K. rigida* Blume (with unarmed ocrea and sparsely armed leaf sheaths) than on those of *K. echinometra* and *K. rostrata*. Although he attributed this result to protection that

ants might afford to the latter species, an alternative hypothesis is that both the plants' growing tips and the ant nests benefit from the armature of ocrea and leaf sheaths. This would not rule out some additional benefit to the plant from its ants. Unfortunately, phylogenetic relationships remain undefined for both plants and ants, and it is not yet possible to determine the extent to which the various relationships between ants and armed *Korthalsia* evolved independently. However, Dransfield's (1981) observation that *Calamus* species of New Guinea and the Philippines show parallel evolution of armed ocrea and relationships with ants suggests that myrmecophytism could have evolved more than once within *Korthalsia* as well. Similarly, myrmecophytic rattans in the genera *Calamus* and *Daemonorops* exhibit parallel evolution of ant galleries formed by interlocking combs of spines, forming collars on the leaf sheaths (Dransfield and Manokaran 1978).

Rates of Resource Supply from Plants

The impact of rates of resource supply on the match between ants and plants is best compared within host genera, holding food type approximately constant. Within western Amazonia, for example, the rate of food body production by *Cecropia* varies across both species and habitat types (Davidson et al. 1991, Davidson and Fisher 1991, Folgarait and Davidson 1992). Faced with competition from fast-growing pioneer species of similar stature, more light-demanding species of large riverine disturbances defer costly defense in favor of rapid growth. Because comparatively shade-tolerant species of small forest light gaps experience light competition from much larger neighbors, diversion of limiting carbon from defense to growth might confer little benefit, and even jeopardize the persistence required to take advantage of later canopy openings. Thus, the more shade-tolerant *Cecropia* species produce swollen stems, prostomas, and trichilia much earlier in development than do their light-demanding close relatives (Fig. 5), as well as producing a greater dry weight of Müllerian bodies per unit leaf area. Despite this greater investment (proportional to the plant's resource budget) in biotic defenses by small gap *Cecropia*,

there are at least three reasons why the absolute rates of food provisioning to ants are greater in light-demanding pioneers than in closely related but more shade-tolerant gap species. First, and perhaps foremost, the smaller sizes of forest gap species at the time of colonization by ants are associated with fewer leaves (sources of food rewards) and slower plant growth rates. Second, even with plant size or light environment held constant, small gap *Cecropia* have intrinsically slower growth and leaf production rates than do their more light-demanding counterparts. Finally, comparatively low light intensities in their typical habitats further limit the capacity of the forest gap plants to produce ant rewards.

Ants appear to respond to these quantitative differences in food production rates of *Cecropia* (Davidson et al. 1991, Davidson and Fisher 1991). For example, in southeastern Peru, patterns of ant associations are more closely tied to habitats than to host identities. Although the closest taxonomic relationships appear to be between *Cecropia* in different habitats (C. C. Berg, personal communication), *Azteca ovaticeps* Forel inhabits only intrinsically fast-growing pioneers of riverine and stream-side habitats. In contrast, specialized *Camponotus*, *Pachycondyla* and *Crematogaster* species, and *Azteca australis* Wheeler are the typical residents of relatively slow-growing and congeneric hosts of small light gaps. Although the latter ants frequently colonize riverine *Cecropia*, they seldom establish colonies there, and they may usually be outcompeted by rapidly developing colonies of *A. ovaticeps*. This pattern holds both within and across host species, and it suggests that ant species may coexist locally by virtue of their "included niches". Species with rapidly growing colonies may dominate higher quality hosts, but be unable to tolerate low rates of resource supply. On the other hand, ants with relatively slow-growing colonies tolerate both high and low quality resources, but are usually excluded by competitors from fast-growing hosts.

A similar pattern of niche differentiation is apparent within plant-ant guilds of other myrmecophyte taxa (including epiphytes) of both the New and Old World (Davidson and Epstein 1989, Davidson et al. 1989 and 1991). For example, specialized *Tetraponera* are the typical resi-

dents of *Barteria fistulosa* Masters growing in small forest treefall gaps, but *Crematogaster* dominate in large clearings (D. McKey, personal observation). In *Barteria nigritana* J. D. Hooker, mostly restricted to light-rich coastal shrub vegetation, *Crematogaster* is the only recorded associate. In *Leonardoxa africana* Aubrév., *Petalomyrmex* is the typical associate of adult trees, and of a large proportion of juveniles. However, juveniles growing in deeply shaded sites are usually occupied by *Catantulus* (McKey 1984). The effects of insolation on resource quality can also be apparent within host species, as in the observation that *Polyrachis* species specializing on broad-leaved bamboos build their pavilions only in sunny areas of bamboo clumps (Dorow and Maschwitz 1990).

At present, factors underlying interspecific differences in the resource demands of ants are poorly studied. However, just as the evolutionary diversification of plants has been influenced by tradeoffs in allocation and life history strategies (e.g., Grime 1974), similar tradeoffs are likely to have contributed to a proliferation of divergent ecological tactics in plant-ants (and ants in general, Tschinkel 1991, A. N. Anderson 1991). Included among these life histories may be: 1) opportunistic (ruderal) species with rapid colony growth rates, high worker turnover, high resource demands, small (or moderate) colony sizes with correspondingly weak colony defense, short colony lifespans, and early reproduction; 2) "tolerant" species with slow-growing colonies, low worker turnover, low resource demands, high longevity, deferred reproduction, and effective defense of the nest site, and 3) competitive species with rapid colony expansion, low worker turnover, and large, long-lived, aggressively territorial and well-defended colonies. The evolution of such divergent ecological strategies is likely to have been influenced also by phylogenetic constraints, such as preexisting uses of exocrine glands (Blum and Hermann 1978, Buschinger and Maschwitz 1984), or the form of the proventriculus, which controls the capacity for and efficiency of liquid food storage and transport (Eisner 1957). Such phylogenetic constraints might help to explain why the competitive rankings and strategies of ants are often well-defined (though not perfectly so) at the generic level.



Fig. 5. Tiny seedling of *Cecropia tessmannii*, whose myrmecophytic traits appear approximately with the fifth through seventh leaves past the cotyledon stage, and when plants are < 10 cm tall. Because of its extreme morphological similarity to *C. membranacea*, *C. (prov.) tessmannii* is still technically lumped with that species (C. C. Berg, personal communication). However, *C. membranacea*, a pioneer of large, riverine disturbances, grows more rapidly and acquires its myrmecophytic traits at substantially and significantly later leaf nodes (Davidson and Fisher 1991).

Other Traits of Weakly Competitive Ants

Appendix 1 reveals numerous exceptions whereby the generic affiliations of ants are imperfect predictors of subordinate or dominant status, as reflected by pruning behavior and association with trichome myrmecophytes or uncontested host plants. Nevertheless, some of these exceptions are consistent with the general principles developed here. For example, despite their chemical defenses, ants in some subgenera of *Camponotus* (especially *Colobopsis* and *Pseudocolobopsis*) can behave as subordinates, living secretive lives inside their hollow stem nests. Yet *Camponotus* of this description occur on a diversity of hosts that lack protective trichomes and, with one exception, they do not prune or attack vegetation around their hosts. At least two factors may explain the capacity of these species to persist on their hosts. First, major workers use their large and often modified heads to seal

stem entrances effectively and to protect nests from invaders. Where ants obtain the majority of their resources from Coccoidea inside stems or domatia (e.g., under ocrea of *Korthalsia*), foraging occurs in seclusion and entails little risk. (A similar explanation may apply to the timid *Pheidole* colonies from myrmecophytic pipers and melastomes, which supply food bodies inside domatia.)

On the other hand, the extrafloral nectar of *Endospermum* and the Müllerian bodies of *Cecropia*, are produced on external plant surfaces. Here, the exclusivity of ant resources is protected in part by the temporary nature or temporal pattern of their production. For example, in the northern coastal forests of Papua New Guinea, *Endospermum labios* Schodde produces almost all of its extrafloral nectar in a brief pulse at about 3:00 AM, likely coinciding with the diel maximum in relative humidity there (Fig. 6). In contrast to myrmecophytic *E. labios*, a myrmecophilic congener, *Endospermum medullosum* L.S. Smith produces a greater fraction

of its nectar during other periods of the diel cycle (D. Davidson, unpublished). Although many *Cecropia* species release Müllerian bodies slowly all day long, they also flush large numbers of these bodies just after nightfall (Davidson and Fisher 1991). Moreover, ants with generalized diets are usually not attracted to the bodies (Rickson 1977, D. Davidson, personal observation). *Camponotus* associates of *Endospermum* and *Cecropia* both forage on leaf surfaces principally at night, and workers of *Anoplolepis* (not a plant-ant) can range freely over *Endospermum* during daylight hours (D. Davidson, personal observation). (See also A. N. Anderson's [1991] discussion of nocturnality in Australian *Camponotus*.) *Cladomyrma* of *Neonauclea* are nocturnal as well (D. Davidson, personal observation), though the object of worker foraging on *Neonauclea* has yet to be identified. Finally, some plant-ants in the genera *Myrmelachista* and *Allomerus* are apparently restricted to their hosts diurnally, but make nocturnal forays to the forest floor (J. Longino, personal communication). Together, these observations suggest that competition may be reduced somewhat at night, though the nature of any restrictions on nocturnal activity in dominants is not readily apparent. While activity schedules of temperate and arid zone ants are strongly related to diel variation in temperature and humidity regimes, biotic selection pressures could be equally important or more important determinants of foraging times in ants of moist tropical forests.

ANCESTRAL VERSUS MODERN RELATIONSHIPS

We have argued that the matching of ants and myrmecophytic plants is convergently alike in different tropical regions, and that this convergence arises from the presence of similarly preadapted plants and ants within the respective biotas. In concentrating on the associations as they exist today, we have neglected the pathways by which they may have reached their present form. Ant-plant symbioses have undoubtedly evolved from more casual and opportunistic relationships between plants and ants. In their initial phases, many of these associations would likely have resembled

modern-day relationships in which plants lack obvious specializations for housing ants (Appendix I, "N" in column 6). Like most other forms of mutualism (reviewed in Thompson 1982), many symbiotic ant-plant mutualisms probably began as parasitisms. What factors may have facilitated the transition from parasitism to mutualism, and what character transformations could have accompanied this change?

For plants hosting ants inside primary domatia (live stems and internodes), ancestral relationships probably consisted of ants tending scale insects within natural plant cavities or in insect borings (cf., Ward 1991). From the start, ants must have benefitted from access to exclusive resources in these protected environments. However, to have remained entirely in the sanctity of the host plant, ants would have needed a well-balanced diet. Homopteran exudates contain not only carbohydrates, but some amino acids and lipids (reviewed in Buckley 1987), and ant colonies are known to harvest and eat Homoptera to meet their protein requirements (e.g., Way 1954, Pontin 1978). Furthermore, in both New and Old World tropics, as well as in Australasia, some plant-ants have evolved means of obtaining added protein and fats from elaborated calluses or heteroplasias caused by traumatic injury to either the inside (*Tetraponera* on African *Vitex*, Bequaert 1922) or outside of host plant stems (South American *Pseudomyrmex* on *Triplaris*, and New Guinea *Camponotus* on *Endospermum* [D. Davidson, personal observation], and possibly Central American *Myrmelachista* on *Ocotea* [J. Longino, personal communication]). In large part then, coccoid-tending residents of live stems and cavities could probably have depended on hosts to satisfy most or all of their nutritional needs, even from the earliest stages of their relationships with these plants.

In contrast, the impact of symbiotic ants on their host plants would have depended on the balance struck between resource losses to scale insects and ants, and any anti-herbivore protection the ants may have originally afforded. Although the majority of ants would probably have provided at least some protection against stem and leaf parasites, the Coccoidea would surely have been a liability. Substantial carbohydrate losses sustained by the



Fig. 6. This large drop of extrafloral nectar was produced in a brief pulse at 3:00 AM on the petiolar nectaries of *Endospermum labios*, at the Christensen Research Station near Madang in Papua New Guinea. (Screenhouse plant courtesy of M. Jebb.)

plants should have been most debilitating to carbon-limited (light-limited) plants. Thus, in habitats of low light intensity, natural selection on plants may have acted mainly to exclude both ants and Homoptera. However, where light was abundant, the benefits of ant defense could have outweighed carbohydrate losses (on average). Natural selection on these plants should have favored attraction of ants, rather than resistance to them. In this way, the propensity of ant-parasitized plants to evolve toward myrmecophytism could have been facilitated by high availability of carbon (light) in relation to limiting mineral nutrients, and impeded when such ratios were low. Furthermore, if herbivore pressures are generally more intense in comparatively productive, sunny environments (see Davidson and Fisher [1991] for *Cecropia*), this trend could have reinforced selection for ant attraction in such habitats.

Although our data set lacks the resolution to test this hypothesis, the hypothesis is consistent with the central result of Schupp and Feener's (1991) recent survey of the distribution of ant attractants (EFN's and pearl bodies) within the flora of Barro Colorado Island, Panama. While the occurrence of

such rewards was clearly correlated with phylogeny, it also appeared to depend on the light environment. Plant families characteristic of forest light gaps were overrepresented among ant-defended families. (See also the frequency of superscripts "e" and "g" in column 2 of Appendix 1.) Schupp and Feener hypothesized that the high frequency of ant defenses among forest gap plants may be explained by the comparatively low costs of producing carbohydrate ant rewards in these light-rich habitats, as well as by the tendency for relatively continuous growth and leaf production in gap species. The latter explanation meshes well with McKey's (1989) interpretation of biotic defenses as an alternative to phenological escape from herbivory (i.e., escape from detection, due to variable and unpredictable new leaf production). Phenological escape would be unavailable to plants with continuous leaf production.

There are some indications that the absence of scale insects may be the derived condition in relationships involving pseudomyrmecines (P. Ward, personal communication). Thus, although Coccoidea can be found at the bases of spines on African and Indian *Acacia* housing *Tetraponera*,

Pseudomyrmex-inhabited Central American *Acacia* lack scale insects but supply protein-rich Beltian bodies. Moreover, the gnawing of internal stem walls by *Tetraponera tessmannii* (Stütz) on African *Vitex*, to produce tunnels with terminal nutritional heteroplasias, could have had its origins in the excavation of pits to increase the feeding efficiencies of coccoids, now absent from this system (see Bailey 1922 for *Cuviera*).

For plants that continued to be inhabited by ants and scale insects, natural selection would be expected to favor a reduction in the ratio of coccoid to ant biomass. Although many obviously specialized ant-plants still harbor Coccoidea (Appendix 1), there is considerable variation across all the ant-plants in the densities of scale insect populations (D. Davidson, personal observation). At one extreme are the comparatively unspecialized relationships between *Anonychomyrma* (previously *Iridomyrmex* [Shattuck, 1992b]) and *Crematogaster* ants, and a number of pachycaulous understory New Guinea trees. Here, the biomass and density of *Cryptostigma* scales are so great that their populations may well be limited by either plant resources or the availability of feeding sites (D. Davidson, personal observation). In contrast, in its more specialized relationship with *Triplaris americana* L., *Pseudomyrmex dendroicus* Forel maintains only approximately one scale insect per leaf junction, and similarly low coccoid densities are apparent in *Cecropia* stems inhabited by *Azteca ovaticipes* and *A. australis*.

By what proximate mechanisms might plants have responded to selection for reducing losses to Homoptera? For myrmecophilic plants, Becerra and Venable (1989) have argued that EFN production could have arisen as a means of paying ants directly and eliminating parasitic homopteran intermediates. Even if EFN's provided ant rewards comparable to or lower in value than homopteran secretions, reduced resource handling times might have induced ants to feed at nectaries and to abandon their Homoptera. In turn, plants would have benefitted from lower rates of infection with homopteran-mediated diseases and possibly lower resource losses. One difficulty with applying this theory to the evolution of myrmecophytes is that it ignores an important distinction between coccoids

(the usual homopteran associates of plant-ants) and EFN's. While EFN's are relatively promiscuous resources, accessible to many ants, coccoids tended inside cavities can be used exclusively by symbiotic ant associates. If the latter ants are the most effective mutualists of the plant, and provide better protection in the absence of opportunistically foraging competitors, selection may favor loss of EFN's. There is evidence for such a scenario in myrmecophytic Asian *Macaranga*, which, in contrast to their non-myrmecophytic congeners, almost completely lack EFN's (Fiala and Maschwitz 1991).

A second difficulty with the hypothesis of Becerra and Venable (1989) is that it ignores the possibility that colonies might keep pace with the added resources (EFN) through short-term redeployment of workers or long-term growth. If so, ants might continue to tend Homoptera while also feeding from EFN's. A plausible alternative hypothesis is linked to the assumption that growth of ant colonies (like that of plants, Bloom et al. 1985) is limited by the ratio of carbon and nitrogen resources. By rewarding ants with abundant carbohydrate but starving them for protein (Carroll and Janzen 1973), plants might have induced colonies to consume the majority of their Homoptera. In support of this argument, *Oecophylla longinoda* is known to consume more coccoids when given a supplemental sugar source (Way 1954). Moreover, M. Anderson (1991) attributes "switching" between predation and mutualism in ant-homopteran relationships (see also Pontin 1958 and 1978) to changes in the nutritional status of the ant colony. If homopteran populations are regulated in response to ratios of carbon and nitrogen availability to ants, colonies might be expected to maintain their associates at densities which supply these resources at optimal ratios for colony growth. Currently, a lack of data prevents further speculation as to how the relative availability (to ants) of carbohydrate and protein might vary with homopteran densities. Future investigations might profitably focus on natural or experimentally induced variation in the relative biomasses of ants and Homoptera in particular ant-plant systems.

PLANT FITNESS IN RELATION TO ANT SPECIES

In many ecological studies of ant-plant symbioses, investigators have focused principally on the question of whether or not a given ant associate benefits its host species. With recently renewed appreciation for the diversity of ants colonizing individual myrmecophytes comes the realization that ants may differ in the protection afforded their hosts (e.g., Janzen 1975, Oliveira et al. 1987, Rico-Gray and Thien 1989, Davidson et al. 1991, Longino 1991a and b, but see Vasconcelos 1990, for a counterexample), and that associations must be studied in the context of community-wide interactions. While existing data are too meager to correlate protection with specific ant traits, some conjectures are warranted. Rapid colony development, large colony size, and high levels of worker activity should enhance host-plant defense. Large insect herbivores (Coleoptera and Orthoptera) may be best deterred by active, large bodied workers (Davidson and Epstein 1989). In contrast, division of colony biomass among numerous small foragers may promote fine-grained searching and facilitate the detection of small prey, for example, lepidopteran eggs (Letourneau 1983, Vasconcelos 1991). Some authors have suggested that small and timid ants provide little protection against herbivores, but augment the nutrient reserves of their hosts through deposits of feces and refuse (e.g., Janzen 1974b, Beattie 1985). However, at least two studies have confirmed the effectiveness of small, docile *Pheidole* ants in defending against either insect eggs (Letourneau 1983), or herbivorous lepidopteran larvae (Vasconcelos 1991). While nutrient enhancement has been demonstrated convincingly in myrmecophytic epiphytes and palms (Rickson 1979, Rickson and Rickson 1986), tests have disputed the theory for the symbiotic associates of *Macaranga* (Fiala et al. 1989) and *Maieta* (H. Vasconcelos and B. Forsberg, personal communication). On reflection, possibilities for nutrient enhancement are limited by the infrequency of foraging off the host (Appendix 1, column 4) and, consequently, by the inability of ants to concentrate materials from the broader environment.

Two other cases are likely candidates for nutri-

ent augmentation by ants (D. Davidson, personal observation). First, certain *Azteca* species center their carton nests on *Tococa* and *Hirtella* species and contribute to a steady rain of carton and refuse at the base of the host tree trunk. Second, as a rheophyte of stream beds and rocky river beaches, *Myrmeconauclea strigosa* (Korth.) Merrill grows with its roots anchored in rock crevices. The *Crematogaster* ants, which are its dominant associates in forests west of Lahad Datu, Sabah, pack refuse and feces into domatia at the distal branch tips, from which new swollen internodes arise. The absence of any obvious food reward (including Homoptera) suggests that ants might leave their hosts to forage. If such is the case, workers could concentrate nutrients which enhance fitnesses of hosts growing in extremely nutrient-poor environments.

In some cases, myrmecophytism actually contributes to host-plant damage by destructive vertebrate predators of ant larvae (especially by woodpeckers [Carroll 1983] and monkeys [Freese 1976, and J. Terborgh, personal communication, for *Cecropia*). Damage by primates may be less common for hosts of ants with powerful stings. First, in Peruvian Amazonia, *Pachycondyla luteola* Roger (the "pungara") is an obligate symbiont of *Cecropia*, and its painful barbed stings reinforce vertebrate learning for a period of seven to ten weeks (D. Davidson, personal observation). Avian preferences for nesting in this (Koeppke 1972) and other myrmecophytes with stinging ants (Young et al., 1990) may be at least partly attributable to the protection which ants afford against primates. Second, the *Tetraponera* of African *Barteria fistulosa* also impressed Janzen (1972) as effective deterrents of vertebrates, and a black colobus monkey avoided ant-occupied *Barteria*, while feeding on an unoccupied individual nearby (McKey 1974). Gray-cheeked mangabey monkeys (*Cercocebus albigena* [Gray]) rip open the branches of this host to prey on *Tetraponera* brood, but only if this can be accomplished by reaching from a perch in a different tree (D. McKey, personal observation). Even large, stinging plant-ants may not affect some vertebrates, however. Gorillas in the Central African Republic feed on *B. fistulosa* leaves and branches apparently undeterred by healthy, active colonies of

Tetraponera (M. Fay, personal communication). Finally, because plant-ants with functional stings also usually prune the vegetation surrounding their hosts, crowns inhabited by such ants are usually sufficiently isolated in forest gaps to avoid the attacks of primates which visit neighboring trees.

TRENDS IN SPECIALIZATION, SPECIFICITY AND COEVOLUTION

Because the evolutionary histories of symbiotic ant-plant systems have been largely independent in biogeographically disjunct tropical regions (McKey and Davidson, in press), intercontinental comparisons may provide general insights into the evolutionary dynamics of such systems. In this section, we discuss evolutionary interactions between ants and plants, focusing on three questions: (1) Has specialization of ants and plants followed similar evolutionary pathways due to parallel and/or convergent evolution in organisms from different continents? (2) Have evolutionary interactions between ants and plants contributed to the generation of diversity in plant-ants and ant-plants? (3) If so, are these interactions a partial cause of intercontinental differences in diversity of ant-plants and plant-ants? Again we focus mainly on the American and African tropics, whose ant-plant associations are best known.

The Nature and Causes of Specificity

Symbiotic ant-plant systems are in general more species-specific than are nonsymbiotic ant-plant interactions (e.g., Schemske 1983). All tropical regions contain examples of ant-plants that are obligately associated with one or a small number of plant-ant species, which in turn have comparably restricted host-plant ranges. In such cases, specificity is doubtless a product of intense evolutionary interaction. However, much of the seeming specificity in ant-plant symbioses may be maintained by ecological processes that require no evolutionary specialization in ant or plant. We have argued that characteristic and repeatedly observed plant-ant matches are the result of species sorting (Jordano 1987) of plants and ants which are mutually pre-adapted in many attributes related to the interaction

(Fisher 1991). Driven by the strong competitive interactions that structure communities of arboricolous ants, the matching of plants and ants is determined by plant and ant traits which modify ant access to plant resources.

In a growing number of ant-plant systems, we now recognize that seemingly specialized plant-ants may be capable of living on any of several hosts, and that many or most myrmecophytes can persist in association with any of several plant-ants. Nevertheless, some relationships are more frequent and/or more durable than others. Understanding the ecological processes which reduce broad potential niches of plant-ants and ant-plants to narrower realized niches is a prerequisite to an evolutionary investigation of such systems (Davidson and Fisher 1991). First, ecological studies suggest simpler alternatives which must be excluded before hypotheses of evolutionary specialization and coevolution can be entertained. Second, if ecological causes of specificity can be defined, these will suggest the likely selective environments in which any evolutionary specialization may have taken place. Third, studies of unusual associations may give clues about the origin of both host-plant specificity and host switches, which seem to have taken place frequently in symbiotic ant-plant systems (Ward 1991).

Evolutionary Specialization of Ants and Plants

If competitive interactions among ants are sufficiently strong and constant, ecological sorting will produce predictable patterns of ant-plant associations and a selective environment conducive to evolutionary specialization (Schemske 1983). Evidence from various tropical regions suggests that evolutionary specialization of ant-plants and plant-ants may have been driven largely by competition among ant species. Even strong pairwise ant-plant mutualisms, it appears, owe many of their traits to an evolutionary background of multispecies antagonistic interactions. Whether these character states were evolved in the context of the symbioses, or merely fine-tuned from pre-existing traits, often cannot be argued confidently from existing data. Nevertheless, many traits of both plant-ants and their hosts may have been elaborated because of

their selective value in the context of symbiotic association.

Ants.—Because ants actively choose their hosts, selection should strongly favor specializations for rapid and efficient host location by queens. In addition to minimizing exposure to predation and other environmental hazards, such adaptations could help to assure priority of access to contested resources. Indeed, competitively inferior ants might even usurp the hosts of more dominant species by evolving rapid means of finding and entering these plants. First, almost nothing is known about the kinds of information that queens employ to locate suitable hosts, but a variety of chemical, visual and other cues may be used at different stages of host identification. Whatever the mechanisms of host identification, the abilities of queens to locate and colonize specific hosts, and their absence from other hosts and habitats (Davidson et al. 1989, Fiala and Maschwitz 1990, Morawetz et al. 1992), provide some of the strongest evidence of evolutionary specialization to the symbiosis. Second, the extreme dorsiventral flattening of the head, thorax and abdomen of *Petalomyrmex* queens could have arisen due to selection for rapid entry of myrmecophytes in the face of intraspecific and interspecific competition for hosts (McKey 1991). Alternatively, however, specialized queen shapes might have evolved first in generalized stem-nesting ants (Longino 1989b), preadapting such ants to become specialized plant-ants. Without additional phylogenetic analysis, adaptations in body shapes remain indistinguishable from preadaptations.

Once foundresses have safely entered a host, their success on plants of different growth rate, maximum size, or lifespan, will likely depend on key energetic, demographic, and life history features of the colony. Intrinsically rapid rates of egg production and development of incipient colonies could be favored on fast-growing plants, and pleometrosis might substitute for this in at least some ant species (Davidson et al. 1991). However, before evolutionary specialization can be inferred from an apparent matching of colony attributes and plant growth rates, careful phylogenetic analysis must exclude the alternative hypothesis that ant traits evolved prior to the origin of the symbiosis. In the case of the *Azteca* and *Cecropia*, this caution is

reinforced by the likelihood that *A. ovaticeps* and its relative *A. alfari*, may have originated from a weedy species which was typical of second growth vegetation (Longino 1991b), and whose life histories could have preadapted it for occupation of relatively fast-growing hosts of riverine succession. In contrast, *A. australis* and its relative *A. xanthochroa* Roger, are probably derived from carton-building ancestors (Longino 1991b), whose comparatively permanent homes may have predisposed them to evolve life history traits typical of modern-day descendants on slower-growing and, in most cases, longer-lived, forest gap *Cecropia*.

Many or most specialized plant-ants appear to have been relatively weak competitors, in which aggressive behavior could well have been maladaptive. Nevertheless, within the limited spheres of their host plants, a number of these ants appear to have evolved greater similarity to dominants, defending absolute territories defined by the boundaries of individual trees. Thus, one scenario apparent in several plant-ant lineages is that of increased colony size and aggression in response to symbiotic association with myrmecophytes (e.g., Janzen 1966). For example, the extended colonies of *Myrmelachista* ants on pure stands of *Tococa occidentalis* (see above) reach an estimated worker population 1-2 million ants (Morawetz et al. 1992). Moreover, on Peruvian *Cecropia*, *Pachycondyla luteola* exhibits the largest and most aggressive colonies achieved by any ponerine ant. Host trees >30 m tall literally seeth with aggressive, stinging workers, and populations almost certainly range into tens or hundreds of thousands of workers (D. Davidson, personal observation). Even if rigorous phylogenetic analysis confirms that closest relatives of these ants have much smaller and less aggressive colonies (as do *Pachycondyla* sp. nov. on Panamanian *Cecropia hispidissima* Cuatrecasas, Davidson and Fisher 1991), ecological studies will be necessary to determine whether the purportedly evolved demographic responses of *P. luteola* are examples of evolutionary accommodation or only plasticity in colony structure. For colonies nesting and feeding in the comparative security of myrmecophytes, increasing worker life spans, and nest sites which grow, rather than decaying (like dead twigs), could lead automatically to larger

worker populations, and greater aggression might follow as a behavioral response to colony size. Similarly, the polygyny and/or pleometrosis noted as typical or occasional in some purportedly highly specialized plant-ants (Janzen 1966 and 1973, McKey 1984, Davidson and Epstein 1989, Longino 1989b, Vasconcelos in press) may be a plastic response to resource availability or competition, since queen number can vary similarly in other ant species (Ward 1989b, Hölldobler and Wilson 1990). Although queens of *Azteca anstralis* found their colonies individually on isolated hosts in small light gaps, they often cooperate to initiate colonies on the faster growing plants of riverine disturbances, where both rates of food supply and competition from other incipient colonies are greater (Davidson et al. 1991). At present it is unclear whether pleometrosis in the latter environment arises from evolutionary adaptation to competition or merely from greater numbers of alates produced and available in that habitat.

Pruning of vines and other vegetation in the vicinities of hosts is one trait which provides less ambiguous evidence for evolutionary accommodation to competition for hosts. Facultative pruning, requiring the presence of enemy ants, may eventually prove to be widespread among unspecialized close relatives of obligate plant-ants. However, both obligate pruning, and the maintenance of vegetation-free zones at the host-plant base, appear to occur predominantly in ants whose highly specialized diets (Janzen 1966, Davidson et al. 1989, Fiala and Maschwitz 1990, Morawetz et al. 1992) and unitary host genera (but see Ward 1991) provide independent evidence for specialization.

A final category of specialized ant traits may have little or no relevance to competitive ability but nonetheless serve as useful indicators of degree of evolutionary specialization in plant-ants. For example, Ward's (1991) phylogenetic analysis of pseudomyrmecines points to trends for plant-ants to have reduced eye size and palpal segmentation, as well as hypertrophied metapleural glands (except in cacia-ants). Palpal segmentation is also reduced in African *Engramma* (now included in *Technomyrmex*, Shattuck, 1992a), in comparison to other dolichoderines from the Ethiopian region (Hölldobler and Wilson 1990). Reduction in anten-

nal segmentation occurs in some lineages of *Allomerus* (Wheeler 1942), and arboreal stem-nesting *Cladomyrma* have fewer antennal segments than do most other formicines (Hölldobler and Wilson 1990). Although 10-merous antennae are characteristic of more generalized *Myrmelachista* species (subgenus *Hincksidris*) which nest in dead stems, specialized Central American *Myrmelachista* plant-ants have antennae with only 9 segments. Lastly, barbed stings are probably derived in both *Pseudomyrmex* ants (Janzen 1966) and *Pachycondyla luteola* (D. Davidson, personal observation). In general, sting defenses may be more effective against solitary vertebrates than against social insect enemies (Davidson et al. 1988), and barbed stings may have evolved under selection to reinforce learning by vertebrate enemies.

Plants.—In myrmecophytes, domatia and various food rewards offer clear support for evolutionary specialization, all the more so since the production of such structures can entail obvious costs. Ecological costs of myrmecophytic traits may be evident in both the presence of ants, as when ant predators open the nests (see above), and in their absence, e.g., when herbivores invade and inhabit foliar or stem domatia (Jolivet 1991, Vasconcelos 1991). Costs are most evident, however, when myrmecophytic traits are lost in the absence of symbiotic ants. For example, though *Cecropia peltata* L. is myrmecophytic throughout most of its distribution, conspecifics in Caribbean island populations lack Müllerian bodies and have trichilia reduced or absent (Janzen 1973; Rickson 1977). (Non-myrmecophytic *Cecropia schreberiana* Miquel might have been mistaken for *C. peltata* on some of these islands [C. Berg, personal communication].) In more recent history, introduced *Cecropia obtusifolia* Bertoloni of Hawaii, and *C. peltata* imported to both Asia and Africa have either lost their Müllerian bodies or trichilia, or are polymorphic for these characters and exhibit a range of trichilia sizes (D. Davidson, personal observation, Putz and Holbrook 1988). Although it could be argued that such losses are determined environmentally, rather than genetically, African populations of *Cecropia peltata* lacked trichilia even when grown from seed in greenhouses, where progeny of myrmecophytic congeners from their native habi-

tats have never failed to produce trichilia (Davidson, unpublished).

Selection may also act on plant characteristics which influence the outcome of ant-ant competition for the resources offered. In so doing, evolution might enhance traits which favor the most effective mutualists (at levels of defense investment optimal for the plant) over their competitors. Perhaps most remarkable, *Piper* ant-plants apparently produce food bodies only when stimulated to do so by the appropriate *Pheidole* ants (Risch and Rickson 1981), or by specialized parasites of the ant-plant mutualism (Letourneau 1990 and 1991). The persistence of Müllerian bodies on *Cecropia* trees lacking specialized ants (Rickson 1977, D. Davidson, personal observation) provides evidence that these bodies are not recognized by unspecialized ants as suitable food. Moreover, Müllerian bodies of at least *Cecropia* (prov.) "*tessmannii*", *Cecropia hispidissima*, and possibly *Cecropia ficifolia* Snethlage appear to have been modified evolutionarily to favor their usual resident ants (Davidson and Fisher 1991).

In a variety of ways, selection might modify the quality, rate, timing or position of the food reward to encourage either fine-grained or coarse-grained foragers, large or small workers, and aggressive, energy-intensive competitive dominants or timid, energy-conservative subordinates (see above). As an extreme example, plants which provision ants with complete diets may facilitate the persistence of weakly competitive species, whose foraging can then be restricted to the host itself (Appendix 1, column 4). At least some species of *Triplaris* induce fine-grained foraging by ants with highly specialized foraging behaviors. These hosts produce pearl bodies which are unique in their yellow color (perhaps indicative of some distinctive nutritional quality) and are distributed in patches on adaxial leaf surfaces. Perhaps pre-adapted for this behavior by prior dietary specialization on pollen and fungal spores (Wheeler and Bailey 1920), the *Pseudomyrmex* residents of these myrmecophytes accumulate these tiny food bodies on their appendages while constantly traversing leaf surfaces. They groom the material frequently onto their sting sheaths, which serve as storage sites until workers return to their nests (Davidson et al. 1988).

In a number of ant-plant genera, food rewards for ants are often produced in more localized and defensible sites on true myrmecophytes than on myrmecophilic relatives with more promiscuous rewards. Thus, in the *Endospermum* of New Guinea (Airy-Shaw 1980), myrmecophilic *E. medullosum* has moderately sized EFN's scattered across abaxial leaves along primary and secondary veins. Petiolar nectaries are only slightly larger. In comparison, myrmecophytic congeners have greatly enlarged petiolar EFN's and all other EFN's greatly reduced in size and number. Similarly, in the genus *Macaranga*, at least some myrmecophilic species have scattered pearl bodies used by a number of unspecialized ants (D. Davidson, personal observation in New Guinea), whereas the most highly evolved myrmecophytes restrict access to food bodies by hiding them beneath recurved stipules. In incipient myrmecophytes, *M. hosei* King ex Hk. f. and *M. pruinosa* (Miq.) Muell. Arg., whose stems are not naturally hollow and are only partially occupied, accessibility of food bodies appears to be intermediate (Fiala et al. 1991). Thus, although food bodies are locally concentrated on stipules, the stipules are horizontal, leaving them exposed. Experimental studies might focus profitably on the outcome of ant-ant competition in relation to the spatial patterning, accessibility and defensibility of ant rewards. Similar relationships are well accepted for other plant-animal mutualisms (e.g., Feinsinger and Colwell 1978).

Restrictive entrances to domatia (Fig. 7) may render these structures more readily habitable by some ants than others, as well as limiting access to stem-dwelling Coccoidea. Prostomas of myrmecophytic *Leonardoxa* are matched to the shapes and sizes of their associated ants (McKey 1991). Urticating hairs on the prostoma of *Cecropia* (prov.) "*tessmannii*" favor large-bodied queens of *Pachycondyla luteola* over smaller-bodied *Azteca* queens (Davidson and Fisher 1991). In general, neither the selective effects of these traits on different ant associates, nor their consequences for plant fitness are well documented. Nor is it often clear where "preadaptation" stops and adaptation begins. For example, the thin pith cavities of myrmecophytic *Vitex* lianes are easily exploited by the plant's specialist associate, the slender

Tetraponera tessmannii, but not by stouter ants of similar body length. At present, however, there is no evidence to suppose that either plant or ant has evolved to produce or enhance such a match. Even the long, elliptical prostoma of *Leonardoxa africana*, matched to the flattened queens of *Petalomyrmex* (McKey 1991), might be explained as preadaptation. As in numerous other ant-plants with stem-domatia, this myrmecophyte's prostoma occurs at the node, opposite the leaf insertion, where a reduction in xylem leaves the stem wall relatively thin (Bailey 1922). In future studies, both field experiments and careful phylogenetic analyses of plant and ant lineages will be required to determine how frequently myrmecophytes may have evolved to influence ant-ant competition.

Limits to Specialization

The forces leading to specialization in ant-plant symbioses are both clear and consistent with theoretical arguments predicting greater specialization in mutualistic systems where strong antagonistic interactions occur among competing mutualists (Law and Koptur 1986). What factors then limit species specificity and account for the persistence of systems in which multiple ants coexist on the same host, or a single ant occupies several hosts? What are the limits to specialization? First, the matches produced by ecological sorting do not necessarily result in mutualistic interactions. A plant may be fortuitously 'preadapted' to harbor a persistent parasite, as well as an effective mutualist. Depending on the match, an association might engender strong reciprocal specialization (when most effective mutualists are paired), asymmetrical specialization, or even antagonistic interactions in which specialization in ants and plants proceeds in opposite directions.

Even when ant-plant associations are fundamentally mutualistic, there may be both genetic and ecological limits to specialization and coevolution (Schemske 1983, Kiester et al. 1984, Howe and Westley 1988). The nature of any genetic constraints is purely a matter for speculation. By and large, we do not know the extent of heritable variation for relevant ant and plant traits, nor whether such variation might limit specialization. Like-

wise, population structure of ant-plants, and especially that of plant-ants, is too poorly understood to support much discussion of how specialization and species origination might take place in these systems. Since sexual selection can drive rapid evolutionary specialization and coevolution in mutualists, added information on ant mating sites and behaviors or data from genetic markers might be especially interesting in helping to determine whether mating could be non-random with respect to the host species where alates originated.

More can be said about potential ecological limits on the intensity of selection for specialization. Most significantly, the outcome of an ant-plant interaction may often depend not only on the specific identities of associates but also on habitat type and plant size. As summarized above, habitat may influence the match between plants and ants through both ecological and evolutionary variation in rates of resource supply to ants. The effects of habitat heterogeneity could also be mediated through other mechanisms that are still poorly understood. For example, on isolated plants, or where nutrient poverty limits productivity and alate production, low frequencies of host plant colonization may reduce the intensity of ant-ant competition for hosts (Vasconcelos, in press, D. Davidson, personal observation). Herbivore pressures on at least some myrmecophytes appear to differ with habitat and plant size (Davidson and Fisher 1991, Janzen 1974a, Letourneau 1983), as does the probability that overgrowing vines will threaten both the host and resident ant colony (Rickson 1977, Davidson and Fisher 1991). Perhaps also varying with habitat are the densities of queen and brood parasitoids, which either kill incipient colonies, or prolong their development (Davidson and Fisher 1991). Finally, the outcome of competition among ants for host plants may be influenced by habitat-correlated physiological effects on colony development. In *Azteca ovaticeps*, queen mortality prior to first worker production is much higher on shaded hosts at the forest edge than on hosts of large, sunny and hot riverine disturbances (Davidson et al. 1991). In both the *Azteca* of South American *Cecropia* and myrmelachistines of African *Leonardoxa*, inter-specific variation in queen color correlates with habitat in a manner consistent with the hypothesis



Fig. 7. Restrictive entrance to domatia of the African myrmecophyte *Leonardoxa africana* (Baill.) Aubrév. (Fabaceae: Caesalpinioideae). The plant's mutualistic ant associate, *Petalomyrmex phylax* Snelling, makes these slit-like entrances at the site of the prostoma, which is of similar shape. The entrance allows access by the specialized dorsoventrally flattened foundresses of *P. phylax*, but not by other ants of similar size. Workers of *P. phylax* are of normal shape, but can easily pass through these entrances because they are much smaller than dealate queens of *Petalomyrmex* or workers of other ant species associated with the plant.

that black queen coloration could be adaptive on fast-growing hosts, possibly because of a positive effect on physiological rates. Queens are black in *A. alfari*, which dominates *Cecropia* of roadsides and pastures in many disturbed regions, and yellowish brown in *A. ovaticeps*, the typical resident of fast-growing riverine *Cecropia* (Longino 1989b). Occurring mainly on *Cecropia* of small forest light gaps, *A. australis* has yellow queens, and may have comparatively slow rates of egg-laying (Davidson et al. 1991). Similarly in *Leonardoxa*, black-bodied queens (and workers) of *Aphomomyrmex* tend to occur in more exposed riverine situations, whereas reddish yellow *Petalomyrmex* are typical of more shaded forest understory.

Within myrmecophyte species, host size-dependent variation in the relative abundances of alternative plant-ants may be determined in some cases by the match between colony resource demands and rates of resource provisioning by the plants. However, other causal mechanisms might also produce correlations between plant sizes and the identities of ant inhabitants. For example, such correlations could occur if ant species differed in the capacity to protect their hosts from herbivory (suggested by Longino 1991a and b, for Central American *Azteca* on *Cecropia*). Additionally, a form of ecological succession may take place, with regular changes in ant inhabitants through individual plant lifespans. Turnover of ant species

through time has been observed on hosts in the genera *Acacia* (Janzen 1975), *Leonardoxa* (McKey 1984), *Tachigali* (Benson 1985), and *Maieta* (Vasconcelos 1990). Just as successional mechanisms may vary across plant communities (Connell and Slatyer 1977), they may also vary across ant-plant systems. One possible explanation for species replacements is that early colonists are eventually replaced by superior competitors (Janzen 1975, McKey 1984, Davidson et al. 1989). In this context, coexistence of multiple ant species on a single host population requires that competitive abilities be inversely proportional to colonizing abilities, with poor competitors making a living as "fugitive species".

Even in the absence of direct interspecific interactions, disparate ant life histories might lead to successional changes among the ants of individual hosts. On Central American *Acacia*, for example, *Pseudomyrmex nigropilosa* Emery is an opportunistic colonist and short-term resident after prior residents have died from fire and other causes (Janzen 1975). A similar mechanism has been proposed by Vasconcelos (1990) to account for the coexistence of *Pheidole minutula* Mayr and *Crematogaster* sp. on *Maieta guianensis* Aublet near Manaus, Brazil. Although the two ant species provide equivalent protection for their hosts, the frequency of *Pheidole* occupancy increases with plant size. Comparatively early death or desertion of hosts by *Crematogaster* (for unknown reasons) leaves plants to be colonized again. Whatever the average relationship between the colonizing abilities of the two ants, larger plants should eventually accumulate *Pheidole* colonies, due to the frequent abandonment of hosts by *Crematogaster*.

To summarize, both the species composition of ant-plant symbioses, and the fitness consequences of particular associations, can vary markedly in space and time. Just as such inconsistencies are postulated to have limited evolutionary specialization in non-symbiotic ant-plant relationships (Schemske 1983, Beattie 1985), they have likely been the predominant obstacles to the evolution of species-specificity in symbiotic associations.

Evolutionary Dynamics of Ant-plant Symbiosis

Given these limitations to species specificity, what are the implications for coevolution? Coevolution has two aspects. The first is co-accommodation, reciprocal evolutionary responses of interacting organisms (Mitter and Brooks 1983). Co-accommodation is most easily recognized when it involves functionally matched characters of associated organisms or coupled character coevolution (Schemske 1983). Several ant-plant systems in both Africa and South America offer examples suggestive of reciprocal specialization of functionally matched characters in plants and associated ants. In this category are matches between the dimensions of ants and the prostomas of their plant associates (McKey 1991, Davidson and Fisher 1991), and between food provisioning by plants and the foraging and pruning behaviors of their ants (Davidson et al. 1988). Though suggestive, the data are not usually sufficient to pass a rigorous test, especially in view of our poor knowledge of phylogenetic relationships (McKey 1991).

The second aspect of coevolution is association by descent (Mitter and Brooks 1983). If ant-plant relationships have persisted and diversified as the associated lineages underwent successive speciation events, their phylogenies should be congruent. If, on the other hand, events such as host-switching and secondary exploitation of preexisting ant-plant mutualisms are frequent, there will be no close correspondence between ant and plant phylogenies. Interspecific hybridization of plants and/or ants will produce yet a third pattern, reticulate evolution. Janzen (1974a) concludes (without rigorous phylogenetic analysis) that the neotropical ant-acacias do not form a tight phyletic group, and postulates that one species may capture ant-adapted traits from another via introgression. Ross (1981) came to similar conclusions regarding African ant-acacias. Aside from the two groups of *Acacia*, there is little information to evaluate the possible role of hybridization in the diversification of ant-plants. Moreover, Janzen's observations might be explained alternatively by genotype-environment interactions. Thus, evolved associations of ants with one acacia lineage could have increased the selection intensity for myrmecophytism in other (possibly preadapted)

lineages, perhaps because ants occasionally colonized these unspecialized hosts.

Of the relatively small number of taxa which have produced modest to extensive radiations of ant-plants or plant-ants, taxonomic uncertainty precludes any examination of the question of association by descent in all but a few cases. And in no case do we have equally robust phylogenies in both ants and plants. By far the best example is Ward's (1991) study of associations between plants and pseudomyrmecine ants, represented by *Pseudomyrmex* and *Myrmecodius* (Ward 1990) in the Neotropics, and by *Tetraponera* in Africa, Asia and Australasia. Specialist plant-ants appear to have arisen at least 12 times in this sub-family, on a wide range of hosts. Most of these events have produced only one or a few species of plant-ants, associated with a comparably small number of host species. Such small radiations offer limited opportunity for association by descent. In some cases, apparently secondary pseudomyrmecine colonizations of pre-existing ant-plant mutualisms have given rise to a small number of species on *Cordia*, *Pleurothrium* and possibly *Cecropia* (Ward 1991), all of which are predominantly associated with other ants (*Allomerus*, *Myrmelachista* and *Azteca*, respectively).

The hosts of pseudomyrmecines do include, however, three plant genera with large numbers of ant-plant species. Each of these (neotropical *Acacia*, *Tachigali*, and *Triplaris*) is associated with a different monophyletic group of *Pseudomyrmex*. Do these more extensive radiations offer evidence of association by descent? Ward (1991) concludes that at the species level, they do not. First, within each of these groups there is no pairwise specificity of ant and plant species. Not surprisingly, there is no clear pattern of cospeciation. Although in each of these three cases, the plant lineage seems to have evolved in concert with the ant lineage, the pattern of associations suggests host shifts within a taxonomically restricted guild of ants and plants, rather than cospeciation. Furthermore, each of these plant groups also harbors ants from at least one other lineage of *Pseudomyrmex*. Even in these extensive radiations from associated ancestors, coevolution seems to have been diffuse, corresponding to the guild coevolution or ecological replacement hy-

potheses (Howe and Westley 1988), rather than to a hypothesis of pairwise coevolution.

Relationships of various plant-ants to neotropical *Cecropia* paint a somewhat similar picture. Within ponerines of the genus *Pachycondyla*, four probable *Cecropia* specialists represent at least three separate origins of specialization on this host genus. Independent origins include species near both *P. villosa* (Fabricius) and *P. unidentata* Mayr (J. Longino, personal communication) as well as *Pachycondyla* sp. nov. in Panama. Of these, the first two species appear to be stem parasites. Their small, secretive colonies show little activity on host surfaces, though workers of at least the species near *P. villosa* harvest Müllerian bodies and locate entrances at prostomas (J. Longino, personal communication). At present, no data suggest specificity of host range within the genus *Cecropia*. In contrast, *Pachycondyla* sp. nov. appears to have a highly specialized relationship with *C. hispiddissima*, which produces especially large, hard and purple Müllerian bodies (Davidson and Fisher 1991, B. Fisher, personal communication). A close phylogenetic relationship between this ant and the Peruvian *P. luteola* cannot yet be ruled out (W. L. Brown, personal communication). Colonies of the latter ant occur only on *C. (prov.) "tessmannii"*, whose relationship to *C. hispiddissima* is currently uncharacterized. The affiliations of *Pachycondyla* sp. nov. and *P. luteola* with their respective hosts are the most likely candidates for pairwise coevolution between ants and *Cecropia* trees, and the evidence is still weak. Even if ant and plant phylogenies turn out to be congruent here, and if speciation events are determined to have been synchronous in ant and plant lineages, any postulated cospeciation would appear to have been minimal, based on the small number of *Pachycondyla* specialized to *Cecropia*.

Three other ant genera provide support for multiple independent colonizations of *Cecropia*. The genus *Camponotus* includes at least two host generalists, *C. balzani* Emery in southeastern Peru, and an unnamed species of *Camponotus* sub-genus *Pseudocolobopsis* in northern Peru (Davidson, unpublished; R. Snelling, personal communication). Multiple radiations of specialized *Azteca* (Longino 1989b, 1991a and b) were mentioned above. Although phylogenies are not yet defined within ei-

ther ant genus, the overlapping and generalized host ranges of closely related ant species argue against cospeciation as the major mechanism by which diversity is generated. Finally, at least one *Crematogaster* species (near *C. curvispinosa* Mayr, J. Longino, personal communication) appears to be a specialist on *Cecropia* in northeastern Peru (vic. Genaro Herrera), but inhabits at least several different hosts within the genus (D. Davidson, personal observation). With specialized symbionts representing four of the five sub-families of plant-ants, and multiple origins within at least three ant genera, *Cecropia* presents a strong case for the ease with which taxa of generalized stem-nesting ants have colonized myrmecophytes over evolutionary time.

Like *Pseudomyrmex* and *Tetraponera*, many other plant-ant genera are associated with numerous, unrelated plant hosts (Appendix 1). Of 31 plant-ant genera (including various subgenera of *Camponotus*), only 11 are known from a single host genus, and three of these are records for species whose specialization as plant-ants (column 7) remains in doubt. As in pseudomyrmecines, these broad generic host ranges are probably due both to multiple independent origins of the plant-ant habit within the ant genus, and to secondary colonization of additional hosts by plant-ant species. However, the taxonomic information necessary to distinguish between these possibilities is lacking. *Allomerus* is a particularly intriguing case. All known species are specialist plant-ants. Unless we assume that non-specialist *Allomerus* once existed but are now all extinct (the genus has no fossil record [Hölldobler and Wilson 1990]), then the host range of this genus (seven plant genera in five families) is due to secondary colonizations and host shifts.

Perhaps the clearest evidence against cospeciation is offered by those cases in which a prerequisite for cospeciation, host-specificity, is not fulfilled. Several plant-ant species are associated with two or more quite unrelated hosts. At least three specialist plant-ant species of *Pseudomyrmex* occupy more than one plant genus (Ward 1991), with *P. viduus* F. Smith recorded from 5 genera in as many families. *Aphomyrmex afer* Emery is associated with *Vitex* (Verbenaceae) and *Leonardoxa* (Fabaceae) (R. Snelling, personal communication). *Technomyrmex* (formerly

Engramma) *kohlii* is associated with five genera (*Cola*, *Scaphopetalum*, *Canthium*, *Diospyros* and *Delpydera*) belonging to four families (Bequaert 1922; R. Snelling, personal communication). These appear to be cases in which secondary colonization of ant-plants has occurred several times.

At least one other case, however, does suggest association by descent. African *Leonardoxa* includes two myrmecophytes, which cladistic analysis has shown to be sister species (McKey 1991). They are inhabited by *Aphomyrmex afer* and *Petalomyrmex phylax* Snelling, respectively, the only two African representatives of the formicine tribe Myrmelachistini. Though these two ants are obviously closely related (Agosti 1991), further taxonomic work will be required to determine whether they are sister species or relicts of formerly diverse genera in which all congeners have gone extinct.

Habitat Specialization and the Generation of Diversity in Ant-plant Symbioses

Our analysis indicates that cospeciation in lineages of plants and of host-specific ants has been infrequent at best. Ant-plant pairs may be co-evolved, but associations seem to be shuffled or broken frequently, rather than diversified in concert via cospeciation. Pairwise coevolution thus can account for little of the diversification of these symbioses. How then have symbiotic ant-plant associations diversified? Mounting evidence suggests that evolutionary interactions in these systems, in both Africa and the Neotropics, correspond more closely to two other models of coevolution, not mutually exclusive, the guild coevolution hypothesis and the ecological replacement hypothesis (Howe and Westley 1988). These hypotheses envisage diffuse evolutionary interactions among sympatric guilds of associated organisms. Speciation may be accompanied by shifts in patterns of host associations, producing new mixes and matches. In these guilds, one member may replace another as the predominant associate of a particular member of the other guild. Guilds are also open. New ants may colonize pre-existing ant-plant mutualisms, perhaps displacing or completely re-

placing other ants, and new plants may join a guild of ant-plants.

We postulate that habitat-dependence in the outcome of different ant-plant interactions has been the principal force driving host shifts and ecological replacements within these guilds. Thus, the main obstacle to species-specificity and pairwise coevolution of ants and plants has at the same time facilitated diversification by other mechanisms.

Host plant quality, as recognized by ants, may vary more with habitat than with host species. Thus, Janzen (1966) has called attention to disparities in the habitat associations of *P. nigrocinctus* (Emery) and *P. spinicola* Emery (= *P. ferruginea*), though the two closely related (Ward 1991) species coexist locally. In some parts of their ranges, these two species also coexist with *P. flavicornis* F. Smith (= *P. belti*), which has yet a different pattern of habitat association (Janzen 1983). In another example, distributions of obligate *Cecropia* ants, both within and across genera, are usually more responsive to habitats than to host species (Harada and Benson 1988, Longino 1989b, 1991a and b, Davidson et al. 1991). As is the case for acacia-ants, the consequent mixing and matching of ants and *Cecropia* species may favor diffuse rather than pairwise coevolution. Likewise, effects of different ants on plant fitness may vary with habitat, for example, if the quality of defense against herbivores mattered less under favorable than unfavorable resource regimes.

Thus, genetic differentiation may be associated more frequently with habitat specialization, both in plants (Davidson and Fisher 1991) and in ants, than with specific identities of associates. However, habitat-dependence may still drive a type of cospeciation. For example, a plant and an associated ant may have parallel genetic responses to environmental variation, both of them diverging from conspecifics in a different habitat. Or, genetic differentiation in one symbiont, driven by habitat specialization, may induce divergence in its associate (Thompson 1987). The likelihood of such events, in which both ant and plant remain associated while undergoing habitat-related divergence, may depend on guild diversity. Thus, when an ant-plant colonizes a novel environment, poor success of the usual ant associate certainly provides selec-

tive pressure for adaptation of the ant to the new habitat. But it also provides opportunities for the establishment of other ant species. The richer the local guild of plant-ants, the greater the likelihood that a member of the guild will establish successfully, replacing the usual associate and preventing its specialization for the novel habitat. In depauperate guilds, preadapted ants are fewer, and the usual associate may be more likely to persist and adapt to the novel environment. A possible example is the relationship between *Leonardoxa* spp. and their *Petalomyrmex* and *Aphonomymex* ants. Plausibly a case of cospeciation, this system involves a small number of ant and plant species (McKey 1991). Neither the two plants nor the two ants ever occur sympatrically, and few other myrmecophytes and domatia-inhabiting ants share their habitats. Perhaps pairwise specificity and cospeciation are more likely to occur in modest and geographically limited radiations such as these, where taxonomic poverty of sympatric guilds of ant-plants and plant-ants offers little scope for host-switching and secondary colonization. The latter processes may dominate in species-rich guilds. If our hypothesis is correct, it would suggest that diversity begets diversity due to genotype-environment interactions in tropical ant-plant symbioses.

EVOLUTIONARY TRENDS IN SPECIES REPLACEMENTS WITHIN PLANT-ANT GUILDS

Host-switching, secondary colonization, and ecological replacement seem to be the predominant modes by which ant-plant associations are modified. Once a new association is forged, it is likely to engender selection on one or both partners, and to give rise to evolutionary diversification. But how do new associations form and spread? What is their effect on preexisting associations? Can we recognize patterns in the radiation of plant-ants and ant-plants? Once again, it may be possible to understand the evolutionary dynamics of ant-plant associations in the context of competitive interactions among ants, and habitat-dependence in the outcome of ant-ant and ant-plant interactions. While many species replacements may have occurred without perceptible trace, contemporary systems in which ant-plants are associated with multiple unre-

Table 2. Earliest fossil records of ants for genera (worldwide) in which specialized plant-ants have evolved (summary excerpted from Hölldobler and Wilson 1990): A = Arkansas amber (USA, middle Eocene); Ba = Baltic amber (northern Europe, early Oligocene); Br = Britain (Oligocene); Do = Dominican amber (Dominican Republic, late Miocene^a); F = Florissant shales, Colorado, USA, Oligocene); Sh = Shanwang shales (China, Miocene); Si = Sicilian amber (Sicily, Miocene).

Sub-family and tribe	Genus	Earliest fossil find
PONERINAE		
Tribe Ponerini	<i>Pachycondyla</i>	Early Oligocene ^{Ba,Br,D}
PSEUDOMYRMECINAE		
	<i>Myrcidris</i>	No fossil record
	<i>Pseudomyrmex</i>	Oligocene ^{D,F}
	<i>Tetraoponera</i>	Early Oligocene ^{Ba}
MYRMICINAE		
Tribe Cephalotini	<i>Zacryptocerus</i>	Late Miocene ^D
Tribe Crematogastrini	<i>Crematogaster</i>	Miocene ^{Si}
Tribe Leptothoracini	<i>Leptothorax</i>	Early Oligocene ^{Ba}
Tribe Pheidolini	<i>Pheidole</i>	Oligocene ^{D,F}
Tribe Solenopsidini	<i>Allomerus</i>	No fossil record
	<i>Solenopsis</i>	Late Miocene ^D
Tribe Tetramoriini	<i>Tetramorium</i>	No fossil record
Tribe Dacetini	<i>Strumigenys</i>	No fossil record
Tribe unclassified	<i>Catanlacus</i>	Miocene ^{Si}
	<i>Podomyrma</i>	No fossil record
	<i>Atopomyrmex</i>	No fossil record
DOLICHODERINAE		
Tribe Tapinomini	<i>Anonychomyrma</i>	No fossil record
	<i>Axinidris</i>	No fossil record
	<i>Azteca</i>	Early Miocene ^D
	<i>Tapinoma</i>	Miocene ^{Si}
	<i>Technomyrmex</i>	Miocene ^{Si}
FORMICINAE		
Tribe Plagiolepidini	<i>Plagiolepis</i>	Early Oligocene ^{Ba,Si}
Tribe Myrmelachistini	<i>Aphomyrmex</i>	No fossil record
	<i>Cladomyrma</i>	No fossil record
	<i>Myrmelachista</i>	No fossil record
	<i>Petalomyrmex</i>	No fossil record
Tribe Camponotini	<i>Camponotus</i>	Early Oligocene ^{Ba,Si}

^a Note added in proof. Although Hölldobler and Wilson (1991) date the Baltic amber as late Oligocene, more recent work summarized by Kirshshna and Grimaldi (1991) suggests an earlier estimate. We use the latter date because it is conservative in relation to our hypothesis.

lated plant-ants may offer examples of species replacements in progress. The various ant associates of myrmecophytes usually occupy different places in a competitive hierarchy. An understanding of their competitive relationships, and how they coexist today, should provide insights into the ecological mechanisms that have driven their evolutionary histories.

Without more phylogenetic evidence than exists today, we have only a snapshot of a process in motion, and cannot know its direction with certainty. Nevertheless, we attempt a provisional distinction between original associates and secondary colonists of several ant-plant associations. First, we focus on two ant lineages which seem to have played predictable and frequent roles in the ecological replacement of primary associates. We then examine likely causes of such pattern, based on what is known of the biology and competitive relationships of the ants involved. Generalizing from these examples, and referencing the fossil record, we propose a hypothesis of taxonomic progressions within lineages of plant-ants. This hypothesis, combined with information on the geological history of mesic-forest environments in different tropical regions, leads to new interpretations of intercontinental differences among ant-plant symbioses.

Directionality of Species Replacements

The primary and secondary associates of many myrmecophytes can be very difficult to distinguish (Ward 1991). Nevertheless, patterns in the biogeographic and taxonomic distribution of host associations in some ant-plant systems suggest that myrmecophytes have been colonized recently by unspecialized arboreal ants or by host-shifting plant-ants, resulting in partial or complete replacement of a prior ant associate. In none of the examples that follow is the evidence for directionality conclusive. Nevertheless, taken together the evidence is strongly suggestive, and the approach has enabled us to propose testable hypotheses and to define critical points where data required to test these hypotheses are lacking.

Crematogaster as Secondary Associates of Myrmecophytes.—Several ant-plant relationships

provide indications that ants of the genus *Crematogaster* have partially or completely replaced prior ant associates of the host plant. First, the pattern of ant associations with the two African *Barteria* species suggests that ancestral host relationships may have involved *Tetraponera* ants. For *T. aethiops* (F. Smith) and *T. latifrons* (Emery), two host-specific associates of *B. fistulosa* Mast. (Janzen 1972), taxonomic isolation from other sections of the genus suggests comparatively ancient origins for the association (P. Ward, personal communication). *Tetraponera* has not been found to inhabit the other described species of *Barteria*, *B. nigritana* Hook. f., which instead houses an apparently unspecialized *Crematogaster*. The latter association may have arisen via secondary colonization of hosts in the more disturbed, light-rich, coastal scrub sites frequented by this plant species. Interestingly, while *B. fistulosa* is occupied by its specialist *Tetraponera* in forest light gaps, it too occurs with unspecialized *Crematogaster* in large, human-made clearings in coastal forests of Cameroon (D. McKey, personal observation).

Second, although *Crematogaster* spp. are presently the numerically dominant associates of East African ant-acacias, *Tetraponera* ants may have been the original inhabitants. Invasion of East African acacias by *Crematogaster*, which generated two new specialists on *Acacia*, may have largely pushed the weakly competitive pseudomyrmecine into marginal high-elevation sites (Hocking 1970). At lower elevations (ca. 900 m), *T. penzigi* (Mayr) appears to be competitively subordinate to *Crematogaster mimosae* (Santschi) and *C. nigriceps* Emery, and has exclusive possession of only 0.7 % of the trees. At higher elevations, it maintains control of up to 8.5 % of host trees. In sites where it cooccurs with the two *Crematogaster*, the pseudomyrmecine appears to persist mainly in unoccupied parts of *Crematogaster*-occupied trees. There it ensures exclusive occupancy of stipular swellings by boring entrance holes too small to accommodate *Crematogaster*, and by plugging or protecting these entrances with carton baffles.

Asian *Macaranga* may be another case where contemporary numerically dominant *Crematogaster* ants have largely replaced the original inhabitants. Poorly known associations occur between two

Camponotus species [provisionally subgenus *Colobopsis*] and both *Macaranga griffithiana* M.A. and *Macaranga puniculata* Gage (Fiala et al. 1990). Each of these hosts grows principally in swamplands (Whitmore 1973 and 1975), marginal habitats where rates of plant growth and supply of ant resources are likely to be reduced. Finally, one *Crematogaster* lineage may also have replaced another. Thus, *Macaranga* hosts in some undisturbed primary forests are occupied by a species with black workers and 11-segmented antennae, whereas hosts of forest and riverine edge typically contain any of an unrelated complex of species with yellowish workers and 10-segmented antennae (D. Davidson, personal observation). Despite habitat segregation under natural conditions, a mixture of the two ant lineages occurs in the extensive *Macaranga* forests left after logging. Clearly, in view of the habitat specificity of both myrmecophytes and their ants, the rapid conversion of primary forests can be expected to alter these symbiotic associations greatly in future years.

In the Neotropics, unspecialized *Crematogaster* are recorded as clear newcomers and secondary associates of several older ant-plant relationships, including those between *Pseudomyrmex* and *Triplaris* (Davidson et al. 1988; Oliveira 1987), *Pseudomyrmex* and *Acacia* (Janzen 1983), and *Azteca* and *Zacryptocerus* with *Cordia alliodora* (R. Carroll, personal communication). These Neotropical examples include no obvious case in which colonization by *Crematogaster* has led to complete replacement of a prior associate, and American *Crematogaster* have only rarely evolved into specialist plant-ants. Included in the latter category are only the *Crematogaster* cf. *victima* of many neotropical leaf-pouch myrmecophytes, and a derivative of the opportunistic and widespread *C. curvispinosa* on *Cecropia* in northeastern Peru (D. Davidson, personal observation).

Azteca as Secondary Associates of Neotropical Myrmecophytes.—In species richness, *Azteca* are the preeminent competitive dominants among New World plant-ants (Appendix 1), and play ecological roles analogous to those of *Crematogaster* in many Old-World systems (Carroll 1983). Like *Crematogaster*, they may be displacing subordinate species in many relationships. For example,

both *Crematogaster* and *Azteca* ants displaced *Pseudomyrmex dendroicus* when permanent wire bridges were made between the host trees and neighboring vegetation (Davidson et al. 1988). Moreover, as we also suspect for Old-World *Crematogaster*, some displacements of primary associates by *Azteca* may have been so thorough that distinguishing contemporary from prior associations is fraught with uncertainty. For example, ants of the genus *Azteca* are the numerically predominant associates of myrmecophytic *Cecropia* today, but associations of *Cecropia* with other ants, such as *Camponotus* and *Pachycondyla*, may be older. Each of these latter genera includes species which are *Cecropia* specialists, and in both cases ongoing competition with *Azteca* may exclude them from riverine and other riparian habitats, where *Cecropia* is most abundant and fast-growing (see above, Davidson and Fisher 1991).

Replacements may also be occurring within the genus *Azteca*. In Amazonian Peru, *Azteca ovaticeps* and its relative, *A. alfari* appear to be relative newcomers, dominating contemporary *Cecropia* populations along riverine and forest edge. The two species are closely allied to ants of other early successional ant plants (Longino 1991b). These ants include *A. foreli* Emery, which inhabits live stems of a variety of rainforest trees, and *A. longiceps* Forel, from mid-elevation *Triplaris* of the Costa Rican Pacific coast. Still other representatives of this species-group occur on *Cordia alliodora*. Thus, *A. ovaticeps* and *A. alfari* may have originated during a comparatively recent host switch onto *Cecropia*. In support of this conjecture are rare observations of apparent mistakes in colony founding behavior. Queens of *A. ovaticeps* occasionally attempt to enter *Cecropia membranacea* by burrowing into the trichilia, rather than into prostomas, even though suitable prostomas are available in uncolonized internodes (D. Davidson, personal observation). The arrival of *A. ovaticeps* may have driven *A. australis* out of riverine environments and deeper into the forest, where it persists on a variety of forest light-gap *Cecropia* species (see above; Davidson and Fisher 1991).

Azteca australis could itself be a secondary colonist. A member of the *A. muelleri* species complex, it is likely descended from generalized

carton-building ancestors with well-defended central nest sites (Longino 1991a and b). Members of this group still maintain carton masses inside the boles of their hosts (Longino 1991a). Ants in this species complex may have gotten their first foothold on myrmecophytic *Cecropia* by building external carton nests on hosts whose prior residents (possibly *Camponotus* and *Pachycondyla* species) had died.

Analogously and in contemporary times, *Azteca* may be invading other myrmecophytic associations. In the Manu National Park and Tambopata Reserve of southeastern Peru, at least two carton-building species (probably *A. ulei* Forel var. *cordiae* Forel and *A. traili* [Emery] var. *tococae* Forel) are residents of trichome myrmecophytes *Cordia nodosa* and *Tococa* spp. (Appendix 1). Queens of both ants initiate their colonies inside domatia covered by protective hairs, and their incipient colonies exhibit host-plant fidelity. Nevertheless, larger, established colonies not only leave their hosts regularly to forage, but build satellite nests (often as ant-gardens) on neighboring trees. These ants also prune trail systems through the protective stem trichomes. On *Cordia*, *Azteca* ants occur mainly on hosts in environments of unusually high light intensity, and conspecific trees in the primary forest understory are occupied by *Allomerus*. If we are correct in assuming that plants with long, dense and erect pubescence became myrmecophytes in the context of persistent occupation by tiny and competitively subordinate ants, then larger-bodied, aggressive and dominant *Azteca* appear to have both restricted the distribution of *Allomerus*, and perhaps eliminated the former residents of *Tococa*. Although *Tococa* is colonized occasionally by timid *Crematogaster* cf. *victima* and a species of *Solenopsis*, we have never found established colonies of these ants on the *Tococa* of southeastern Peru.

Identifying and Characterizing Dominants

Crematogaster and *Azteca* are the two genera for which biogeographical and phylogenetic information is most suggestive of a frequent role as secondary colonists in species replacements among plant-ant guilds. They are also the preeminent

competitive dominants in the arboreal ant faunas of Africa and Asia, and New World tropics, respectively. Isolated from these continents, the Australian tropics (including New Guinea and associated islands) contains a unique set of competitive dominants and relative newcomers to ant-plant symbioses. Among these ants (all dolichoderines) are two genera previously classified as *Iridomyrmex* (Shattuck 1992b), but now considered to be distinct taxa and endemics of either the Australian (*Anonychomyrma*) or Oriental and Australian regions (*Philidris*). Also included are pantropical *Technomyrmex* (a single species of which is apparently native to the New World, Shattuck, 1992a).

Several other kinds of evidence substantiate the inferential evidence about the relative competitive abilities of ants involved in ant-plant symbioses. Field experiments have demonstrated that *Crematogaster* and *Azteca* are the principal formicid enemies of New World *Pseudomyrmex* on *Triplaris* (Davidson et al. 1988, see also Oliveira 1987). Furthermore, both host-plant fidelity and pruning of host-plant neighbors are indicative of weak competitive ability (Davidson et al. 1988, 1989) and occur with some frequency in *Pseudomyrmex*, *Tetraponera*, *Pheidole*, *Camponotus*, and in various myrmelachistines. In contrast, these behaviors are atypical of *Crematogaster*, *Anonychomyrma*, *Azteca*, and *Technomyrmex* (Appendix 1, column 4). Rare occurrences are limited to early successional environments where vines and competitors are particularly threatening, as for the *Azteca* of New World *Cecropia*, and *Crematogaster* of Asian *Macaranga*. They can also characterize ants which are unusually timid for their genera, as are the *Azteca* exhibiting host-plant fidelity on pubescent species of *Triplaris*.

Implicit in their capacity to invade myrmecophytes previously dominated by other ants, secondary colonists likely owe their success to evolutionary novelties which have enhanced their colonizing and/or competitive abilities. The genera listed above as competitive dominants are alike in possessing potent exocrine products which help to convey competitive superiority in interactions with other ants (Blum and Hermann 1978, Buschinger and Maschwitz 1984). Structural characteristics of waists and gasters permit workers to elevate gasters

and direct toxins toward enemy ants. The same adaptations can be effective against potential nest raiders, as when *Crematogaster* workers seal hollow stem nests with protruding gasters bearing poison droplets on modified spatulate stings (Forel 1928). Many dominants are also carton-builders, which monopolize resources in the arboreal zone by constructing primary or ancillary nests over Homoptera and other localized food sources such as extrafloral nectaries.

These traits contribute to the capacity of dominant ants to monopolize "promiscuous" plant rewards such as EFN's and surface-feeding Homoptera, which are either totally unprotected or only partly secluded beneath clasping or folded stipules of myrmecophiles. Thus in Borneo, *Crematogaster* species dominate the exposed EFN's of most individuals of myrmecophilic *Endospermum* (Euphorbiaceae), *Ryparosa* (Flacourtiaceae), and *Macaranga aetheadenia* Airy Shaw (D. Davidson, personal observation). *Crematogaster* are also preeminent among visitors to other myrmecophilic Malaysian *Macaranga* spp. (Fiala and Maschwitz 1991). In New Guinea, scale-tending *Crematogaster* are the numerically predominant inhabitants of the stout hollow stems of weedy *Nauclea* (D. Davidson, personal observation). Myrmecophiles with nectaries partly secluded beneath folded or clasping stipules include New Guinea *Archidendron* (Fabaceae) and Oriental *Shorea* (Dipterocarpaceae), both often dominated by *Technomyrmex* ants (D. Davidson, personal observation, Tho, *vide* Maschwitz and Fiala, in press). By sealing off the folded stipules with carton, these ants may restrict their competitors' access to EFN. An ability to monopolize externally located food resources may also confer a competitive advantage to dominants on myrmecophytes which produce such resources. This result would be especially likely if evolutionary interactions of the plants with prior ant associates had led to increased size and/or number of EFN's and food bodies, or otherwise increased the rate of food production to a level at which the plant becomes attractive to competitive dominants requiring high rates of resource supply.

Processes of Species Replacements

How have secondary colonists managed to replace primary associates with highly evolved mechanisms for locating and exploiting hosts? Even very aggressive and dominant ants may have difficulty evicting weakly competitive ants, once the latter have established their colonies. Thus it seems likely that many secondary colonists first achieved access to myrmecophytes by occupying hosts whose usual partners were absent for one reason or another. For example, like the *Azteca* discussed above, some *Crematogaster* could have gained a preliminary foothold on myrmecophytes by building carton nests on plants which had outlived their ant colonies. Early stages of this scenario may be represented in the New World associations of *Crematogaster* with myrmecophytic acacia species in second growth environments (Janzen 1983). Although *Crematogaster* are apparently unable to replace *Pseudomyrmex* on smaller acacias, they can resist colonization by the latter species on larger acacias which have lost their former *Pseudomyrmex* colonies.

The more characteristic ant associates may be absent for other reasons. First, by opening domatia to feed on ant larvae, vertebrate predators of ants may make these domatia unsuitable for continued habitation by weakly competitive species. For example, after swollen internodes of *Cordia alliodora* are opened by woodpeckers, unspecialized *Crematogaster* often move in and employ carton baffles to seal breaks in the domatia (R. Carroll, personal communication). Second, older domatia are frequently abandoned by the usual residents, as colonies move to follow new growth and productivity. In *Cecropia* (Davidson et al. 1991), *Remijia* (Benson 1985), *Leonardoxa* (D. McKey, personal observation), *Endospermum*, *Korthalsia*, and other genera (D. Davidson, unpublished), such abandoned domatia are often occupied by unspecialized ants, which gain at least protected nest sites if not food (Davidson and Fisher 1991, Longino 1991a). A possible case of progressive specialization in such ants may be seen in the unnamed *Crematogaster* species which occupies *Cecropia* near Genaro Herrera in Loreto, Peru (D. Davidson, personal observation). Related to *C. curvispinosa*

(J. Longino, personal communication), it is apparently descended from generalized stem-nesters, rather than from a carton-building lineage. Specialization on *Cecropia* could have been favored by selection sharpening the host-finding abilities of foundresses which occasionally colonized the woody bases of forest-gap plants, and eventually evolved to recognize Müllerian bodies as food.

Third, the typical ant associates may fail to either colonize or to persist on hosts in inappropriate habitats. Small forest light gaps are marginal for western Amazonian *Cecropia*, and comparatively low colonization rates on isolated and inconspicuous gap plants appear to have provided safety for refugees from riverbanks, as well as opportunities for *in situ* colonization of this host genus. All four little-known genera of *Cecropia* ants persist principally in forest light gaps. Both *Camponotus balzani* and *Pachycondyla luteola* colonize riverine plants, but rarely persist there, being excluded by *Azteca*. In contrast, species of *Crematogaster* and *Camponotus* (*Pseudocolobopsis*) occur on several light gap species at Genaro Herrera, but apparently do not even colonize plants of riverine and forest edge. Their relationships with *Cecropia* may have evolved *in situ*. Alternatively, past competition with *Azteca* may have led to a shift in their habitat preferences.

Finally, colonists may also gain a foothold at the latitudinal or elevational limits of ant-plant associations. Latitudinally, the genus *Triplaris* ranges northward into Mexico; in southwestern Chiapas near Mapastepec, it is occupied by a variety of apparently unspecialized species of *Azteca*, *Crematogaster* and *Pseudomyrmex*, rather than by the more typical specialized pseudomyrmecine associates (D. Davidson, personal observation). At least one specialized *Cecropia* ant, dry forest *A. coeruleipennis* Emery, may have evolved *in situ* in Central America (Longino 1989a and b), a peripheral and comparatively species-poor region within the overall distribution of *Cecropia*. These events might well have resulted from independent secondary colonizations of a host which reached Central America from South America in advance of its typical ant symbionts, or which colonized habitats unsuited to the usual associates.

Elevational segregation among plant-ants of particular hosts suggests that new colonizations might occur at the elevational limits of species distributions. In the lowlands of Cameroon, myrmecophytic *Leonardoxa* consistently house one of two closely related myrmelachistine ants, *Petalomyrmex phylax* or *Aphomyrmex afer*, depending on host species (McKey 1991). However, in submontane forests of the Rumpi Hills (500-1700 m), where neither of these ants occurs in association with *Leonardoxa*, the plants are inhabited by a bewildering array of other ants, including at least two species each of *Crematogaster*, *Axinidris* and *Technomyrmex*, and one species each of *Tapinoma* and *Leptothorax* (R. Snelling, personal communication). Some of these ants are known not to be host-specific, and they may be secondary colonists of a preexisting association of *Leonardoxa* with myrmelachistine ants, although firm conclusions on directionality of this shift must await further work. Finally, in the Neotropics, altitudinal replacements should be common at the periphery of the Andes. Although we know of no published data to test this prediction, Longino (1991b) relates that the ranges of some *Azteca* residents of *Cecropia* segregate altitudinally, with some species occurring as high as 2000 m in elevation.

As secondary colonists of myrmecophytes become increasingly specialized for exploiting their new hosts, selection should enhance the host-finding abilities of these species. With their priority-of-colonization eroded, primary associates may eventually be displaced to marginal habitats or replaced altogether.

Taxonomic Progressions Within Plant-Ant Lineages

Since ant-plant symbioses have been shaped by repeated evolutionary colonizations and strong competition among ants, major taxa of plant-ants might be expected to exhibit regular taxonomic progressions in species distributions and characteristics. Similar progressions have been described for adaptive radiations in several well-studied animal groups, including ants (Wilson 1959a and 1961), carabid beetles (Erwin 1985), and birds (Ricklefs and Cox 1972; Diamond 1986). These accounts are related

in their emphasis on competition as the force driving evolutionary trajectories in animal lineages. Wilson's seminal exposition of the "taxon cycle" in Melanesian ants proposes that ants invade new geographic areas principally via marginal habitats where competition from other ants is reduced. From this tenuous foothold, and driven by arrivals of new and more dominant species, they diversify and evolve competitive strategies which eventually enable their invasion of more species-rich forest habitats. In apparent contrast, Erwin's recent account of "taxon pulses" in carabid beetles proposes that young carabid taxa first appear in productive and central moist equatorial habitats. There, they force the specialization and migration of older taxa into less competitive peripheral latitudes and habitats. Apparent disparities in the phrasing of Wilson's and Erwin's theories obscure their common ground. Both ideas have their roots in Darlington's (1957) "centrifugal speciation", whereby intense biotic interactions drive waves of species and higher taxa from tropical to temperate regions. Moreover, whether species originate in new and permissive environments, or as evolutionary novelties in biotically restrictive environments, young species are those with "r-selected" life histories, and generalized and expanding distributions. Older, progressively "K-selected" species are driven by biotic interactions to increasing specialization and more circumscribed distributions. There they persist by either unique strategies for evading natural enemies, or by tolerance of unfavorable conditions. Vermeij (1978) has argued cogently for similar evolutionary trajectories in various marine invertebrate taxa.

The evolutionary history of plant-ants strongly suggests similar taxonomic progressions. Three types of evidence support such an interpretation. First, as discussed above, taxonomic and biogeographic patterns in some ant-plant symbioses suggest directionality in species replacements, and particular taxa occupy predictable roles as victims (e.g., Pseudomyrmecinae) and agents (e.g., *Crematogaster* and *Azteca*) of such replacements. Second, and also discussed above, field experiments and observations strongly support interspecific competition among ants, often habitat-dependent in its outcome, as the principal mechanism of

species replacements. Furthermore, roles of different ants in postulated replacements are consistent with their status (independently determined) in competitive hierarchies. Third, within ant-plant guilds, the postulated replacements of subordinate genera, such as *Pachycondyla*, *Plagiolepis*, *Camponotus*, *Pseudomyrmex*, and *Tetraponera*, by dominant genera such as *Crematogaster*, *Technomyrmex*, and *Azteca*, are consistent with the historical sequence in which these taxa are represented in the fossil record (Table 2, based on Hölldobler and Wilson 1990, and see below).

The diversification of ant taxa began in earnest no later than the beginning of the Tertiary Period (Hölldobler and Wilson 1990), and it eventually made ants the most important natural enemies of one another. At protected nests and feeding sites, timid, twig-inhabiting myrmelachistines and pseudomyrmecines, probably among the earliest plant-ants, sought out pubescent plants or insect borings and other cavities of live plants. But in the background, competition was escalating. Evolutionary advancements in offensive and defensive weaponry intensified the pressures on timid and secretive plant-ants. As discussed above, evolutionary novelties and secondary colonizations appear to have arisen differentially in environments where disturbance favored weedy species with early and high reproductive allocation, superior colonizing ability, and thus priority of access to ant domatia. Here also, high productivity (associated with high light intensities) subsidized rapid colony growth and the evolution of costly chemical weaponry. Individually or in combination, these traits made their bearers formidable enemies of existing plant-ants, driving them into ever more restrictive specialization on one or a few hosts, into marginal habitats, and in some cases into extinction. Eventually, many secondary colonists appear to have partly or completely replaced the primary associates of several myrmecophyte lineages. These secondary associates were often pressured in turn by successive waves of newly evolved dominants.

What examples support such a scenario? Myrmelachistine ants provide perhaps the best illustration of the fate of an old group of competitively subordinate ants, whose members have been driven to suboptimal habitats, to extreme special-

ization, or to extinction, by dominant ants. As circumscribed by Hölldobler and Wilson (1990), following Wheeler (1920), this tribe is pantropical and includes six genera, two of which are endemic to each of the major tropical regions (the New World, tropical Africa and the Oriental tropics). In a recent and still incomplete analysis of generic relationships in Formicinae, Agosti (1991) casts doubt on the monophyly of the tribe, placing *Cladomyrma* in a different informal genus-group from all the others. We follow the usual treatment of the tribe, but acknowledge the need for further work to resolve phylogenetic relationships of these ants.

Myrmelachistine genera have no fossil record (Table 2), possibly because most have long been specialist plant-ants with restricted ecological distributions. However, they are likely to have been widespread prior to Miocene times, since two ant genera from a tribe (Gesomyrmecini), considered by Wheeler (1920) to be closely related (but see Agosti 1991), are represented in early Oligocene Baltic amber (Hölldobler and Wilson 1990). One of these, *Gesomyrmex*, is represented by four extant species of the Oriental region (Wheeler 1929a). They share with the Oriental myrmelachistine *Cladomyrma* certain similarities, such as reduced antennal segmentation (believed to be a derived character) and worker polymorphism with major, media, and minor workers. Furthermore, *G. kalshoveni* Wheeler of Java, is recorded as nesting in twig cavities of *Artocarpus* in primary forest (Wheeler 1929b). These bits of information on an ant genus regarded by Wheeler (1929a) as "living fossils which have undergone no significant modification since the Early Tertiary" suggest that the plant-ant habit may have a long evolutionary history in the Formicinae, currently regarded as having diverged very early from the basal lineage of the Formicidae (Hölldobler and Wilson 1990).

In all parts of their pantropical distribution, myrmelachistines appear to have experienced ecological contraction. Although no phylogeny is available for the New World genus *Myrmelachista*, interspecific patterns in its distribution and ecology reveal the likely imprint of past competition. *Myrmelachista* are often conspicuous leaf foragers in montane forests of Central and South America,

where dominant *Crematogaster* and *Azteca* ants are largely missing (J. Longino, personal communication). In sharp contrast, congeners of tropical lowlands are stem-nesters with a relatively inconspicuous presence on leaf surfaces. Among residents of Costa Rican *Ocotea*, workers of a *Myrmelachista* plant-ant at 500-700 m elevation (at Rara Avis) do not attack vines (B. Fisher, personal communication), though those of a congener at 50 m in nearby La Selva Biological Station do prune (D. Davidson, personal observation). Finally, in western Amazonia, perhaps the center of neotropical ant diversity (Wilson 1987), *Myrmelachista* residents of *Duroia hirsuta* and *Cordia nodosa* appear to protect themselves not only by pruning vegetation other than potential host plants, and by maintaining extensive clearings ("supay chacras"), but by effectively hiding from larger-bodied ants amid the dense stem hairs of these two hosts. (Morawetz et al. [1992] argue that creation of similar clearings by a *Myrmelachista* species on *Tococa* is not a product of past competition. However, this assertion is based strictly on the probably valid assumption that clearings enhance the light environment and productivity of host plants; it did not stem from any direct test for the effects of competition from other ants [see, e.g., Davidson et al. 1988]). Overall, the pattern reveals that increasing specialization for resisting dominant ants may have been required for persistence in highly competitive and diverse lowland rainforest faunas.

The evolutionary fortunes of myrmelachistines also appear to have declined in the Old World tropics. In Africa, they are represented by only two monotypic genera (*Petalomyrmex* and *Aphomyrmex*). The former is restricted to a single host species and confined to a very small area of Lower Guinea coastal forest. Both species are plant-ants, though interestingly, neither prunes nor inhabits pubescent myrmecophytes. *Cladomyrma* is one of two myrmelachistine genera known from Asia (with the status of *Pseudaphomyrmex* remaining uncertain), and all five described species are specialized plant-ants (Agosti 1991). Some of their hosts (e.g., *Saraca*) are shared with *Crematogaster*, suggesting the potential for competitive interactions with this group of dominant ants. Furthermore, patterns of host association indi-

cate that *Crematogaster* may have replaced *Cladomyrma* in some systems. Thus *Cladomyrma* persists on Asian *Neonauclea*, but *Crematogaster* dominates closely related *Myrmeconauclea*. Too little is known of phylogenetic relationships among representatives of any of these lineages to draw firm conclusions.

Pseudomyrmecines appear to be another relatively old group in which the plant-ant habit may be ancient, and in which competitively subordinate plant-ants have been restricted or replaced by more recently evolved, competitive dominants. *Tetraponera* first appears in fossil deposits in the early Oligocene and *Pseudomyrmex* in the Oligocene (Table 2). The monotypic *Myrcidris*, a plant-ant whose specializations indicate a long history of association with plants, may be a relict that is the sister group to all other pseudomyrmecines, though other interpretations are possible (Ward 1990). As discussed above, plant-ants of this relatively old subfamily are among the most frequent apparent victims of the expansion of younger groups such as *Crematogaster* and *Azteca*.

Other groups of competitively subordinate ants for which there is circumstantial evidence of replacement by more recently evolved dominants also occur relatively early in the fossil record. These include *Pachycondyla*, *Camponotus*, and *Plagiolepis*, all of which appear in the early Oligocene. *Cecropia* specialists derived from widely distributed *Pachycondyla villosa* and *P. unidentata* (J. Longino, personal communication) are probably more recent secondary colonists, inhabiting mainly older and woody stems abandoned by other ants. At present, no evidence indicates that these are replacing former inhabitants. *Allomerus*, another genus being pressured by contemporary dominants, has no fossil record, perhaps because all of these ants have been plant-ants with highly restricted distributions.

In contrast to these weakly competitive groups, genera implicated as dominant ants and secondary or tertiary colonists of existing associations appear to be more recent arrivals. The first fossil records of *Crematogaster* and *Technomyrmex* are in the Miocene, and *Azteca* appears in the early Miocene (Table 2).

Taxonomic Progressions and Intercontinental Comparisons of Ant-Plant Symbioses

If taxonomic progressions such as those postulated above play major roles in transforming ant-plant symbioses over evolutionary time, then long-term evolutionary history assumes an added dimension as an important factor shaping intercontinental differences in the nature of ant-plant symbioses. Contemporary patterns will reflect the point to which taxonomic progressions in plant-ants have proceeded in a region. The location of this point should depend on the ages of regional mesic-forest communities (to which most ant-plant symbioses are restricted), the traits of the particular dominant and subordinate ants evolved there during this period, and the degree to which the region is isolated from the products of taxonomic progressions begun elsewhere.

West Gondwanaland, today represented by its derivative continents Africa and South America, has been considered the cradle of the angiosperms (Raven and Axelrod 1974). Mesic tropical forest and its typical constituents, including plant-ants, have had a long history on both these continents. In Africa, for example, despite climatic vicissitudes and shifts in continental position, a large area of lowland tropical rain forest has persisted unbroken since the Late Cretaceous-Paleocene (75-55 my B.P.) up to the present (Axelrod and Raven 1978). That taxonomic progressions in Africa and South America began with similar starting material, and have continued for about the same amount of time, may account for many of the striking similarities in ant-plant symbioses of these two regions (McKey and Davidson, in press). Interestingly, these two continents share old, competitively subordinate ant groups like myrmelachistines and pseudomyrmecines. Although these taxa would respond in analogous ways to the later onslaught of dominants, the dominants are derived from different genera on the two continents. Whereas in the Neotropics, the preeminent competitive dominants consist of endemic *Azteca*, *Crematogaster* dominate in the Old World, where they are much more prevalent than in the American tropics (Appendix 1).

During virtually all the Tertiary, South America was an island continent (Barron et al., 1981, Gentry 1982). Perhaps the later appearing dominants, *Crematogaster* and *Acteca*, evolved long after direct exchange between the two continents (via overland connections or island filter bridges) became impossible. Evidence suggests that *Crematogaster* could be an Old World genus which arrived relatively late in the New World, possibly as part of a widespread tropical Laurasian biota, elements of which could have reached the Neotropics via North America. First recorded in Sicilian amber in the Miocene, the genus is represented in Dominican amber (late Miocene), and might conceivably have invaded South America via Panama, a connection in place since the Pliocene (Keigwin 1978, Barron et al. 1981, Marshall et al. 1982). Moreover, species richness of *Crematogaster* is greater in the African and Oriental tropics than in the Neotropics (Brown 1973), and the genus has evolved numerous specialized plant-ants in the former two regions, but only two such described species in the American tropics. From our summary in Appendix 1, relationships involving *Crematogaster* account for only 7.6 % of all 66 symbiotic ant-plant relationships listed for the Neotropics, but 39.5 % of 43 associations and 27.3 % of 33 relationships in Africa (including Malagasy) and the Oriental tropics, respectively. Based on analyses at the generic level, our calculations fail to take into account the substantial radiations of species within the genus *Crematogaster* on Asian *Macaranga* (Appendix 1), as well as the nine species of *Crematogaster* occurring on African *Musanga* (though probably none is a specialized plant-ant). No parallel radiations occur in the American tropics.

During the Tertiary, while the South American biota was evolving in isolation, there were repeated opportunities for biotic exchange between tropical Africa and tropical Laurasia. The latter region has long harbored mesic tropical forests, though opinions vary on whether these forests are as ancient as those of West Gondwanaland (Raven and Axelrod 1974). At the very least, the Oriental tropics were an area of moist, equable climate relatively removed from the major vicissitudes of Neogene and later climatic change (Raven and Axelrod 1974).

Biotic connections of tropical alliances, at least through the early Tertiary, may account for similarities in taxonomic composition of both subordinate and dominant plant-ants of the African and Oriental regions (e.g., *Tetraponera* as well as *Crematogaster* and *Oecophylla*). They may also help to explain some possible cases of common ancestry among ant-plant associations of the African and Oriental tropics (McKey and Davidson, in press).

Of the major tropical regions, the Australian tropics (northern Australia, New Guinea, and associated islands) are outstanding for the geologic youth of their tropical mesic-forest environments. By the Paleocene, Australia was connected with the rest of the world only by a cool-temperate pathway to South America via Antarctica (Raven and Axelrod 1974). At the start of its northward movement 45-49 my B.P., what is now tropical northern Australia was all well south of the Tropic of Capricorn, and was still 10 degrees south of its present position by the Miocene, when direct migration from the Asian tropics first became possible (Axelrod and Raven 1972). As for New Guinea, neither it nor its principal antecedents existed prior to about 40 my B.P. Only by the Miocene did it lie close enough to the proto-Indonesian arc to begin receiving large numbers of immigrants from tropical Asia. (However, as vertebrate distributions illustrate, such migration was never directly overland [Axelrod and Raven 1982]). Thus tropical northern Australia and mesic-forest portions of New Guinea have been populated to a large degree by taxa derived from the Asian tropics via intervening islands (Wilson 1961; Raven and Axelrod 1974). Nevertheless, the contemporary distributions of at least some plant-ants (e.g., *Anonychomyrma*, see Shattuck, 1992b) reveal an almost certain origin in Australasia.

Tropical forests of northern Australia and New Guinea provide uniquely little evidence for replacement of older and competitively subordinate ant genera by contemporary dominants. The origins of tropical rain forests in the Australian region have apparently been too recent to have allowed significant radiations of specialized plant-ants in more ancient and weakly competitive ant genera prior to the arrival and expansion of the dominants. If so, this could help to explain why the fraction of

ant-plants obviously specialized as myrmecophytes is so low in the Australian region (column 6 in Appendix 1). Compared to 51.2 % of 39 Neotropical ant-plant genera, 59.4 % of 32 African genera, and 41.4 % of 29 Oriental myrmecophyte genera, only 10.7 % of 28 such genera in the Australian region have conspicuous specializations to attract ants. In the last of these areas, only *Endospermum*, *Canthium* and *Calamus* have convincingly ant-attractive traits (Appendix 1). Present day plant-ants of this region consist principally of dominant species of *Anonychomyrma* (formerly included in *Iridomyrmex*, Shattuck 1992b), *Technomyrmex* and *Crematogaster*, as well as *Philidris* on epiphytic myrmecophytes (Shattuck 1992b). These ants occupy only a small number of variously preadapted host genera, where they maintain scale insects at remarkably high biomass, possibly limited by stem volume. Consistent with their status as dominants, they do not exhibit host fidelity in foraging. Neither pruning of host-plant neighbors, nor hiding among dense trichomes is required for persistence of such capable competitors. Two associations with weakly competitive ant genera may also be comparatively recent in origin. The *Camponotus* of *Endospermum* obtain their protein not from specially evolved plant structures, nor from protected sources within the stem (e.g., homoptera or the heteroplasias of, e.g., *Vitex*), but through a form of parasitism of external stem walls, i.e., the induction of heteroplasias from cambium (D. Davidson, personal observation). Moreover, at least one proposed myrmecophyte in this genus often occurs without its ants (Airy-Shaw 1980). Similarly, Ward (1991) notes that the unnamed *Tetraponera* tending coccids in terminal branches of *Cupaniopsis* has a much narrower geographic range than does its host, and that the symbiosis is apparently young.

In attempting to explain intercontinental differences in diversity, it will be extremely difficult to distinguish the relative importances of two major historical factors. These are regional differences in 1) the condensation of diversity through competition; and 2) the magnification of diversity, as affected by habitat diversity and its effects on rates of evolutionary host shifts and *de novo* evolutionary colonizations (see above and McKey and Davidson, in press.).

CONCLUSIONS

Similar selection pressures acting on correspondingly preadapted ants and plants have produced strikingly parallel and convergent evolution in the symbiotic ant-plant relationships of different tropical regions. Although current concepts of ant-plant coevolution focus on the pairwise interaction between ant and host plant, these alone cannot account for the patterns we observe. Even in relationships where pairwise interactions are undoubtedly strong, multispecies interactions appear to have determined many features of present-day symbioses. The most important force driving the evolutionary biology of ant-plant symbioses is interspecific competition among arboricolous ants. Plants differ in the kinds of resources which they offer to ants, in the rates at which they supply these resources, and in traits which influence the relative competitive abilities of foraging and nesting ants. As in other communities structured by competition, plant-ants sort out across plants in ways that are predictable from their particular resource requirements and competitive abilities and the spectrum of available resources (see also Bristow 1991). In the American, African and Asian tropics, competitively dominant ants are associated with the most light-demanding and fast-growing hosts, which supply resources at the rates required to fuel rapid colony growth, interspecific aggression and other traits required for dominance. In contrast, competitively subordinate ants are restricted to plants which supply resources at rates too low to support dominant ants, or to those from which dominant ants can be excluded by long, dense plant hairs, pruning of neighboring vegetation, or by other ant and plant traits which favor competitively subordinate species. Competitive interactions among ants determine whether patterns of ant-plant association are sufficiently predictable for strong interactions to shape the evolution of ants and plants. When competitive interactions in plant-ant guilds result in constancy in the pairing of particular ants and plants, reciprocal evolutionary interactions may occasionally give rise to pairwise coevolution.

Parallel and convergent selection pressures acted on similar biological material on different tropical land masses. In American, African, Asian and

Australian regions, the same important preadaptations facilitated evolution of the plant-ant habit in several lineages of arboricolous ants. Foremost among these traits were the habit of tending Coccoidea, and the differential competitive abilities determined by generically typical offensive and defensive weaponry, or by inherent colony growth rates and other life-history attributes. Likewise, similar sets of plant traits facilitated the evolution of myrmecophytes on different continents. Structures evolved independently of ant-related selective pressures were co-opted repeatedly as myrmecophytic traits in plant lineages that eventually produced ant-plants. These traits included both the long, dense hairs typical of many myrmecophyte stems and domatia, and stems strongly thickened as support structures for large leaves, and available as nest sites for opportunistic ants. These similarities in starting material have rendered even more pronounced the striking parallel and convergent evolution of ant-plant symbioses in the New World and Old World tropics.

Diversity of both myrmecophytes and their attendant ants appears to accumulate mainly across habitats, rather than biogeographical regions (McKey and Davidson, *in press*). Among ant-plants, evolutionary diversification across habitat boundaries often appears to reflect the conflicting selection pressures imposed by different plant resource environments. Like other tropical plants (McKey et al. 1978, Coley 1983), myrmecophytes have responded evolutionarily to particular resource regimes by altering their relative investments in defense versus growth and, perhaps, their relative allocation of different kinds of resources to defensive function (Davidson and Fisher 1991, Folgarait and Davidson 1992). In turn, ecological and evolutionary responses of plants to different resource environments determine the quantity and quality of resource supply to ants. On the whole, then, both partners in ant-plant associations may be more sensitive to habitat than to taxonomic differences among symbiotic partners.

Strong competition among mutualists has been proposed as a major factor driving the evolution of specialization in mutualisms (Law and Koptur 1986), and it could help to account for the origins of many specialized ant-plant symbioses. Neverthe-

less, where sufficiently well-studied, phylogenies of plant-ants, together with host distributions of these ants, suggest that pairwise coevolution and cospeciation have been rare. Rather than simple, pairwise ant-plant systems, guilds of interacting ants and plants seem to be the most frequent arena of ant-plant evolutionary interaction. Perhaps as a consequence, plant-switching and secondary colonization (rather than cospeciation or some other form of association by descent) may have been the usual processes by which these mutualisms diversified. Repeated colonization of myrmecophyte taxa has occurred as unspecialized ants have exploited preexisting mutualisms and specialized plant-ants have switched hosts. Habitat-dependence in the effect of associations on fitness of the participants seems to have been the principal force leading to the evolution of new associations. The motor driving such evolutionary opportunities was likely the climatically induced range expansion that placed ants or plants into habitats sufficiently novel to change selection regimes, and to increase encounters with new associates (McKey and Davidson, *in press*).

Regardless of how species originate, a complex mosaic of habitats should help to maintain higher local diversity, with greater species richness of myrmecophytes and/or specialist plant-ants, and a greater number of ant/plant combinations. Since the potential for evolution of new associations via host shifts and secondary colonization depends in part on the sizes of locally interacting ant and plant guilds, high local diversity may lead to higher rates of species origination. Thus, independently of distributional changes driven by varying climates, beta-diversity is likely to have enhanced alpha-diversity.

As summarized here, the determinants of diversity of plants and ants in these symbiotic mutualisms will likely generalize to other components of tropical floras and faunas. In particular, we expect that diversification of tropical plants has often involved evolutionary adjustments in the amounts and kinds of defenses, in response to habitat differences in absolute and relative availabilities of essential resources. Consequently, habitat mosaics related to edaphic factors and incident solar radiation should often determine mosaics in the primary productiv-

ity available to consumer organisms. Habitat specialization to different productivity regimes has likely been important to both the generation and maintenance of diversity in many tropical consumer guilds whose member species have strongly overlapping resource requirements (cf., Terborgh 1983 for primates, and S. Robinson and J. Terborgh, personal communication, for birds).

Habitat specialization may frequently also represent the intermediate and final stages of a taxon pulse, in which new, opportunistic, abundant, and widespread species are driven to progressively greater specialization, finer niche differentiation, diminished distribution and abundance, and perhaps even eventual extinction (Wilson 1959a and 1961, Ashton 1969, Erwin 1985, Diamond 1986). If taxon cycles or pulses are general features of animal and plant lineages, they might aid in explaining patterns in the relative abundance distributions of taxa within higher taxa. Dial and Marzluff (1989) have discussed the frequency of "hollow curve distributions", or the overdominance of particular minor taxa within major taxa (subunits/unit). Thus, the degree of dominance of most dominant taxa is greater than that predicted by a variety of null models based on Poisson processes, random cladogenesis, and simultaneous or sequential resource subdivision, and it is compounded at lower levels of the taxonomic hierarchy. Taxon pulses might regularly give rise to such patterns if the enumeration of taxa at successively lower levels of the taxonomic hierarchy (where taxa are more numerous) were more likely to pick up comparatively rare groups which had recently acquired evolutionary novelties, and which represented intermediate stages of a taxon pulse.

Our analyses of the evolutionary dynamics of ant-plant symbioses here and elsewhere (McKey and Davidson, in press) lead us to propose new hypotheses to explain differences in the diversity of ant-plants and plant-ants across different tropical regions. Such disparities are quite pronounced between the American and African tropical regions, where ant-plant symbioses are best understood. Previous explanations for differences in the biodiversity of species-rich Neotropical and depauperate African rain forests have emphasized the contrasting climatic histories of these two regions.

Focusing on range contractions during periods of unfavorable climate, these explanations attribute Africa's lower diversity to greater extinction during the Pleistocene, as Africa's climate became drier, and refugia were fewer than in Amazonia (Raven and Axelrod 1974). We propose that differences between the two regions in the rates of species origination may be at least as important as extinction rates. The relatively stable geological history of most of Africa, including the rainforest zone, has created a landscape with relatively little elevational relief (hence few sharp spatial contrasts in temperature and rainfall), comparatively little edaphic variation, and relatively infrequent and spatially limited fluvial disturbance. In contrast, the Andean orogeny, and subandean tectonic activity, have helped to create a landscape of great elevational, climatic, and edaphic complexity, especially in western Amazonia. This has resulted in a complex and dynamic mosaic of habitats. Colinvaux (in press) suggests that species origination usually takes place when ranges are re-expanding during periods of climatic amelioration. If this is so, then in the Neotropics, especially in western Amazonia, range expansion would be much more likely than in the African forest zone to place ants and plants into novel habitats, leading to speciation, the formation of new associations, or both.

Although poorly known by comparison, Asian rain forests occur in regions (especially Borneo) where topography is substantially more variable than that of tropical Africa. Aided by forest fragmentation on numerous island land masses, this topography has contributed to the diversification of several myrmecophyte lineages here. Myrmecophyte diversity in Asia appears to be intermediate between that of the African and American tropics. On the other hand, both regions of the Old World tropics may have had the generic diversity of their plant-ant faunas condensed, relative to that of the New World, by the comparatively early arrival of a new wave of competitively dominant *Crematogaster*. The relatively recent origin of rain forests in the Australian tropics (including New Guinea and associated islands) appears to have limited the diversification of myrmecophytes in all but the epiphytic Hydnophytinae (Jebb 1991, Huxley and Jebb 1991). In addition, the elaboration of

myrmecophytic traits, which have evolved so frequently elsewhere in associations with weakly competitive ants, may have been limited in Australia by the cooccurrence of contemporary dominant and subordinate ants at the time when rain forests were evolving.

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Appendix 1. Summary of ants living regularly in symbiotic association with one or more host species. Questionable or missing data are indicated by question marks. Columns:

(1) Ant genera (superscript ^{CT} indicates carton-building typical of the genus, though not necessarily of plant-ant species) in biogeographic regions (N) = Neotropical, (E) = Ethiopian, (M) = Malagasy, (O) = Oriental, and (A) = Australian regions.

(2) Host taxa have growth forms: T = tree; U = treelet or understory tree; S = shrub; L = liana or vine, R = rattan, B = bamboo and H = hemiepiphyte. Habitats include: b = mountain brooks; e = edge, second growth, riparian environments; g = forest light gaps; l = littoral scrub; p = primary forests; s = savannahs or dry forest, and a = aguajals or swamps.

(3) Ants nest in domatia comprised of: L = leaf pouches; S = naturally hollow stems; Sp = pithy stems, hollowed by ants; I = swollen internodes; P = swollen petioles or bases of petioles; Ps = petiolar sheath; R = swollen rachi and petioles; St = persistent stipules (inflated or folded); Sh = persistent spathe; Th = swollen thorns; F = swollen flowering shoots; G = gall-like swellings; C = carton shelters around domatia, folded leaves, and/or hairs or spines; Cl = cavity formed by leaf base clasping stem; B = insect borings; O = inflated ocrea (proximal extension of leaf sheath beyond the petiole), A = erect, narrow auricles on each side of petiole, at the terminus of the sheath; Ac = acanthophylls, or basal pinnae reflexed backward to form a secluded cavity at the base of a palm frond; Ga = galleries enclosed by interlocking combs of spines, forming collars on leaf sheaths, and T = vast chambers excavated inside tree trunks by ants and partitioned by carton. Plant pubescence: y = domatia and stems bear long, dense hairs or spines, likely to inhibit movements of larger bodied ants; n = such hairs or spines lacking, or s = only a subset of plants have these hairs.

(4) Ants prune vines and vegetation around their hosts: Y = obligate for plant-ants in this genus; S = in at least some ant associates of the host genus; F = where known, pruning is facultative, i.e., in the presence of enemy ants; N = not yet reported for the ant genus on this host genus. Host fidelity (foraging predominantly or entirely on the host): y = yes; n = no; i = for young (incipient) but not established colonies.

(5) Food types include: P = pearl bodies; B = other specialized food bodies; H = exudates and bodies of homoptera (Coccoidea); E = extrafloral nectar; N = floral nectar; G = uncharacterized exudates of tiny glands; F = fungi; W = lipid-rich and/or protein-rich plant wounds, or heteroplasias caused by traumatic injury by ants; O = pollen; T = glandular trichome.

(6) Plants have evolved apparently specialized structures to house ants: Y = yes; N = no.

(7) Estimated number of congeneric ant species found regularly on the host genus; probability of more (+) or several more (++) indicated parenthetically. Square brackets denote ants known to be unspecialized, or whose specialization is in doubt.

(8) References for data on ants or plants: Bq = Bequaert 1922; W = Wheeler 1942; S&B = Schnell and Beaufort 1966; B = Benson 1985; H = Huxley 1986; J = Jolivet 1986; H&W = Hölldobler and Wilson 1990; D = Davidson et al. 1989; IP = in press; PC = personal communication, DD and DM = respective author's observations.

Appendix 1

(1) Ant Taxa	(2) Host Taxa, Growth Form and Habitat	(3) Nest in	(4) Ant Traits	(5) Food Type	(6) Spec. Myrm.	(7) # Ant Spp.	(8) References
PONERINAE							
Pachycondyla (N)	CECROPIACEAE <i>Cecropia</i> ^{T,ag}	S.n	SF,y	BP	Y	3[1]	Davidson & al., 1991; J. Longino PC
PSEUDOMYRMECINAE							
Myrmecoris (N)	MYRTACEAE <i>Myrcia</i> ^{U,p}	S.n	?y	H	Y	1	Ward 1991 &/or PC
Pseudomyrmex (N)	BORAGINACEAE <i>Cordia</i> ^{Te}	Ln	?y	H	Y	3	" + Ward 1990
(N)	CECROPIACEAE <i>Coussapoa</i> ^{H,e?g?}	??	??	?	?	1	" ; W
(N)	EUPHORBIACEAE <i>Sapum</i> ^{T,e?g?}	Sp.n	?y	E?H	N	1	"
(N)	FABACEAE <i>Acacia</i> ^{S,sepp}	Th.n	S,y	BE	Y	12	" + Janzen 1966, 1974a; Manriques & Dirzo 1990
(N)	<i>Pithecellobium</i> ^{T,se}	S.n	?y	E(?)H	Y?	1	" + Ward 1989a
(N)	<i>Platymiscium</i> ^{T,?}	??	??	H?	N	2(+)	" + W
(N)	<i>Pterocarpus</i> ^{T,ea}	FR,n	??	?	Y	[1]	" + Forel 1904; Spruce 1908; Rojo 1972
(N)	<i>Tachigali</i> ^{T,jag}	P,n	S,y	H	Y	9(+)	

LAURACEAE									
(N)	<i>Ocotea</i> ^{US,p}	Sp.n	?,?	H	N	1	"		
(N)	<i>Pleurothrium</i> ^{US,p}	Sp.n	?,?	H	N	1	"		
POLYGONACEAE									
(N)	<i>Ruprechtia</i> ^{US?}	S.n	?,?	H?	Y?	[1]	" + Spruce 1908; B. Brandbyge 1990		
(N)	<i>Triplaris</i> ^{T,egg}	S.n	S,y	HFW	Y	6(+)	" + DD; Davidson & al. 1988; Brandbyge 1986		
BIGNONIACEAE									
<i>Tetraponera</i>									
(E)	<i>Stereospermum</i> ^{T,?}	Sp.n	?,?	HE(?)	N	1	" + Bq; J		
(O)	<i>Stereospermum</i> ^{T,e}	Sp.n	?,?	HE	N	[1]	DM		
FABACEAE									
(E)	<i>Acacia</i> ^{S,s}	G.n	?,?	HE	Y	1	Ward 1991; Hocking 1970		
(O)	<i>Acacia</i> ^{S,s}	Th.n	?,?	HE	Y	[1]	T. Musthak Ali PC; P. Ward PC; DM		
(M)	<i>Mimosa</i> ^{S,s}	Sp.n	N,y	H	N	1	P. Ward PC		
GRAMINEAE									
(O)	<i>Gigantochloa</i> ^{B,e}	B?.n	?,?	H	N	1	P. Ward PC		
PASSIFLORACEAE									
(E)	<i>Barteria</i> ^{T,egg}	Sp.n	Y,y	HFOWE ^{b,y}		2	Ward 1991; Janzen 1972		
SAPINDACEAE									
(A)	<i>Cupaniopsis</i> ^{T,s}	Sp.n	?,y	H	N	1	"		
VERBENACEAE									
(E)	<i>Vitex</i> ^{L,e}	Sp.n	?,y	FW	N	1	" + Bq; J		
MYRMICINAE									
Tribe Cephalotini									
^s <i>Zacryptocerus</i>									
(N)	BORAGINACEAE	I.n	N,y	?	Y	1	Carroll 1983; W; J. Longino PC		
	<i>Cordia</i> ^{T,egg}								

FABACEAE									
(N)	<i>Platymiscium</i> ²	?,?	?	N	1	B; W			
Tribe Solenopsidini (provisional)									
<i>Allomeris</i> ⁴¹									
(N)	BORAGINACEAE								
	<i>Cordia</i> ^{U,p}	1,y	PH	Y	4(+)	W; B; D; D. Yu PC			
(N)	CECROPIACEAE								
	<i>Pourouma</i> ^{U,p}	P,y	B	Y	1	B; Berg & al. 1990			
(N)	CHRYSOBALANACEAE								
	<i>Hirella</i> ^{U,p}	L,y	E	Y	1(+)	B; Prance 1972, 1989			
(N)	MELASTOMATACEAE								
	^d <i>Tococa</i> ^{U,pc}	L,y	H	Y	3(+)	W; B; Herre & al. 1986			
(N)	^e <i>Clidemia</i> s.s. ^{S,a}	L,y	GH	Y	1(+)	B			
(N)	RUBIACEAE								
	<i>Duroia</i> ^{U,e,2g?}	L,y	?	Y	1(+)	B; Wheeler & Bequaert 1929			
(N)	<i>Remijia</i> ^{U,e}	L,y?	?	Y	1(+)	B; Schumann 1890			
<i>Solenopsis</i>									
(N)	GESNERIACEAE								
	<i>Besleria</i> ^{S,p}	L,y	?	Y	1	B; H			
(N)	RUBIACEAE								
	<i>Duroia</i> ^{U,eg}	L,y	?	Y	1(+)	Wheeler & Bequaert 1929			
(N)	<i>Hoffmannia</i> ^{S,p}	L,y	?	Y	1	B; H			
<i>Monomorium</i>									
(O)	<i>Myrmeconaulcea</i> ^{S,e}	1,n	?	Y	[1]	Maschwitz & al., 1989			
Crematogastrini									
<i>Crematogaster</i> ⁴¹									
(N)	<i>Cecropia</i> ^{T,g}	S,n	BPH	Y	1	DD			
(E)	<i>Musanga</i> ^{T,e}	S,n	H	N	[9+]	Duviard & Segeren 1974			

(E)	<i>Barteria</i> ^{T₁pe}	I,n	?;?	HFOWE ^b Y	Y	[1+]	Bq; S&B; DM
(E)	<i>Barteria</i> ^{T₁l}	I,n	N;?	HFOWE ^b Y		[1+]	Bq; S&B; DM
RUBIACEAE							
(E)	<i>Canthium</i> ^{T₁ae:U₁p}	I,s	?;?	H	Y	[1+]	Bq; DM; S&B
(E)	<i>Civiera</i> ^{U₁p}	I,s	?;?	H	Y	1(+)	Bq; DM; S&B
(E)	<i>Gardenia</i> ^{T₁ae}	L,n	?;?	HE	N	[1]	DM; S&B
(O)	<i>Myrmeconauclaea</i> ^{S₁e}	I,n	?;?	?	Y	1	Ridsdale 1978; Maschwitz & al., 1989
(E)	<i>Nauclea</i> ^{T₁a}	I,n	?;?	H	Y	[1+]	Bq; S&B
(O)	<i>Neonauclaea</i> ^{T₁S;?}	I,n	?;?	H	Y	1(+)	Bq; J; Ridsdale 1978
(E)	<i>Psychotria</i> ^{S₁e}	S,n	?;?	H	N	1(+)	S&B
(E)	<i>Rohmannia</i> ^{T₁p?}	I,s	?;?	H	Y	1(+)	Bq; S&B
(E)	<i>Uncaria</i> ^{L₁eg?}	I,n	?;?	H	Y	1(+)	Bq; S&B
RUTACEAE							
(O)	<i>Zanthoxylum</i> ^{U₁e}	S,y	?;?	?	Y	[1]	Maschwitz & Fiala 1992
SAPOTACEAE							
(E)	<i>Delpyodora</i> ^{U₁p}	L,y	?;?	?	Y	1(+)	DM
VERBENACEAE							
(E)	<i>Clerodendrum</i> ^{U₁e}	S,n	?;?	E?	Y	[1+]	J; H; S&B
BORAGINACEAE							
<i>Cordia</i> ^{U₁p?}							
(N)	GESNERIACEAE	I,y	?;?	P	Y	1(+)	W; B
<i>Besleria</i> ^{S₁p}							
(N)	MELASTOMATACEAE	L,y	?;?	?	Y	1	B

Pheidolini

Pheidole^{ca}

(A)	<i>Chisocheiton</i> ^{U,p} RUBIACEAE	B,n	N,n	HW?	N	I(+)	Stevens 1978; Mabberley 1979; DD
(A)	<i>Canthium</i> ^{?,?} FABACEAE	Sp,n	N,y	H	Y	I	G.B. Monteith & P. Flower PC
(E)	<i>Leonardoxa</i> ^{U,p} RUBIACEAE	I,n	?,?	E	Y	I(+)	DM
(E)	<i>Caviera</i> ^{U,p} MELASTOMATACEAE	I,n	?,?	?	Y	I(+)	Bq; DM
(O)	<i>Myrmecontauclaea</i> ^{S,se} MELASTOMATACEAE	I,n	?,?	H	Y	[I+]	Maschwitz & al., 1989
(N)	<i>Wasnania</i> DOLICHODERINAE	L,y ⁱ	N,n	H	Y	[I]	Tennant PC; DD
Tapinomini	<i>Anonychomyrma</i> MELIACEAE	Sp,n	N,n	H	N	I	Warburg 1894; M. Jebb PC
(A)	<i>Aphananixis</i> ^{U,p} MELIACEAE	B,n	N,n	H	N	I	Stevens 1978; M. Jebb PC
(A)	<i>Chisocheiton</i> ^{U,p} MONIMIACEAE	I,s	N,n	H	?	I(+)	Bq; J; Philipson 1984
(A)	<i>Steganthra</i> ^{U,p} MYRISTICACEAE	I,n	N,n	H	N	I(+)	Bq; Foreman 1978; J; DD
(A)	<i>Myristica</i> ^{U,p} MYRTACEAE	T,n	N,n	H	N	I(+)	Monteith 1986 & PC; DD
(A)	<i>Syzygium</i> ^{T,leg} PALMAE	Ga,n	N,?	H	N	I(+)	DD; Ridley 1910
(O)	<i>Daemonorops</i> ^{R,p} SAPINDACEAE	O,s	?,?	?	Y	I	Beccari 1884
(O)	<i>Korthalsia</i> ^{R,p} SAPINDACEAE	?,?	?,?	H	?	I(+)	M. Jebb, <i>fide</i> H
(A)	<i>Mischocarpus</i> ^{U,p} FABACEAE	I,n	?,?	E	Y	[2+]	R. Snelling PC; Shattuck 1991; DM
(E)	<i>Leonardoxa</i> ^{U,p}						

<i>Aztecac</i> ^{vi} (N)	BORAGINACEAE	I,n	N,?	H	Y	4-5	W; Carroll 1983; Manriquez & Dirzo 1990
<i>Cordia</i> ^{T,e}							W; B; D
(N)	<i>Cordia</i> ^{u,p,g}	I,y ⁱ	N,i	HG	Y	2-3+	
(N)	CECROPIACEAE						
	<i>Cecropia</i> ^{T,eg}	S,n	S,y	BPH	Y	13(++)	Bq; W; Davidson & Fisher 1991; Longino 1991b; Manriquez & Dirzo 1990
(N)	<i>Coussapoda</i> ^{U,e,g?}	?,?	?,?	?	?	[1]	Forel 1904
(N)	CHRYSOBALANACEAE						
	<i>Hirtella</i> ^{U,p}	L,y	N,?	E	Y	1(+)	B; Prance 1972; DD
(N)	FABACEAE						
	<i>Ormosia</i> ^{T,e}	S,n	N,?	?	N	1(+)	B; H
(N)	^a <i>Tachigali</i> ^{T,eg}	P,n	?,?	H	Y	1-2	W; B
(N)	FLACOURTIACEAE						
	<i>Tetrathylacium</i> ^{U,pe}	S,n	?,?	H	N	[1+]	Tennant 1989
(N)	LAURACEAE						
	<i>Pleurothrium</i> ^{U,p}	Sp,n	N,n	H	N	1(+)	D; H. van der Werff PC
(N)	MELASTOMATACEAE						
	<i>Clidemia</i> s.s. ^{S,e}	L,y	?,?	H	Y	1(+)	B
(N)	ⁱ <i>Sagraea</i> ^{S,e}	L,y	?,?	?	Y	1(+)	B; W. Judd PC
(N)	<i>Tococa</i> ^{U,pe}	L,y ⁱ	N,i	H	Y	2(+)	W; B; D
(N)	POLYGONACEAE						
	<i>Triplaris</i> ^{T,p}	S,y	N,y	G	Y	1,[1]	W; D
(N)	RUBIACEAE						
	<i>Duroia</i> ^{U,e}	L,y	?,?	?	Y	1(+)	Wheeler & Bequaert 1929
(N)	<i>Duroia</i> ^{U,e}	I,y	N,i	G?H	Y	1	DD
(N)	<i>Remijida</i> ^{S,p}	B,n	N,n	?	N	[1]	B

<i>Tapinomelet</i> ^{cf}	FABACEAE						
	<i>Leonardoxa</i> ^{U,p}	I,n	?,?	E	Y	[1]	R. Snelling PC; DM
	<i>Humboldtia</i> ^{U,p}	I,n	?,?	HE	Y	[1]	DM; T. Musthak Ali PC
<i>Technomyrmex</i> ^{cf}	CECROPIACEAE						
	<i>Poikilospermum</i> ^{L,e}	Sp,n	N,?	H	Y?	[1]	D. Samson PC; R. Snelling PC
	EBENACEAE						
(E)	<i>Diospyros</i> ^{U,p}	L,y	?,?	HE	Y	1	R. Snelling PC; Letouzey & White 1970; DM
	FABACEAE						
(A)	<i>Archidendron</i> ^{U,g}	StC,n	N,n	E	Y?	[1]	DD; de Wit 1942; Verdcourt 1979
(O)	<i>Humboldtia</i> ^{U,p}	I,n	N,?	E	Y	[1]	F. Rickson PC
(E)	<i>Leonardoxa</i> ^{U,p}	I,n	?,?	E	Y	2(+)	DM
	MYRISTICACEAE						
(A)	<i>Myristica</i> ^{U,p}	I,n	N,n	H	N	1(+)	J; DD; Beccari 1884
	RUBIACEAE						
(E)	<i>Canthium</i> ^{L,e}	I,y	?,?	?	Y?	1(+)	Bq; DM
(E)	<i>Cuviera</i> ^{S,p}	I,n	?,?	H	Y	1	Bq
(E)	<i>Cuviera</i> ^{U,p}	I,s	?,?	?	Y	1(+)	Bq; DM
(E)	<i>Ixora</i> ^{U,p}	L,n	?,?	?	Y	1	DM; D. Olson PC
	SAPOTACEAE						
(E)	<i>Delpyodora</i> ^{U,p}	L,y	?,?	?	Y	1	R. Snelling PC; DM
	STERCULIACEAE						
(E)	<i>Cola</i> ^{SU,pe}	L,y	?,?	?	Y	1	Bq; Nkongmeneck 1985; DM
(E)	<i>Scaphopetalum</i> ^{SU,p}	L,y	?,?	?	Y	1	Bq; Dejean et al. 1990; DM
FORMICINAE							
Myrmelachistini							
<i>Aphonomymex</i>	FABACEAE						

(E)	<i>Leonardoxa</i> ^{U,p}	In	N,y	H	Y	1	McKey 1984; 1991
(E)	VERBENACEAE						
	<i>Vitex</i> ^{T,e}	Sp.n	?,?	H	N	1	R. Snelling; DM
<i>Cladomyrma</i>	CRYPTERONACEAE						
(O)	<i>Crypteronia</i> ^{T,p}	Sp.n	?,?	HE	Y?	1	U. Maschwitz & al. 1991
	FABACEAE						
(O)	<i>Milletia</i> ^{L,?}	S,?	?,?	H	Y?	1	U. Maschwitz & al. 1989
(O)	<i>Saraca</i> ^{T,e}	In	?,?	HE	Y?	1	U. Maschwitz & al. 1991
	RUBIACEAE						
(O)	<i>Neonauclea</i> ^{U,e}	In	S,y	H	Y	1+	R. Snelling PC; DD
<i>Myrmelachista</i>	BORAGINACEAE						
(N)	<i>Cordia</i> ^{u,p,g}	I,y	Y,i ^e	GH	Y	1(+)	Campbell et al. 1989; DD
	LAURACEAE						
(N)	<i>Licaria</i> ^{T,p}	Sp.n	?,?	H	N	3(+)[2]	J. Longino PC
(N)	<i>Ocotea</i> ^{U,p}	Sp.n	S,y	GH	N	6(+)	J. Longino PC; DD; H. van der Werff PC; Manriquez & Dirzo 1990
(N)	<i>Pleurothyrium</i> ^{U,p}	Sp.n	N,y	H	N	1(+)	J. Longino PC; D; H. van der Werff PC
	MELASTOMATACEAE						
(N)	<i>Miconia</i> ^{?,?}	?,?	?,?	?	?	[1]	B; Forel 1904
(N)	<i>Tococa</i> ^{SL,e}	L,y	Y,i	T	Y	1	Campbell et al. 1989 Morawetz et al. 1992; Svoma and Morawetz 1992
	MELIACEAE						
(N)	<i>Guarea</i> ^{T,p}	Sp.n	N,y	H	N	2(+)[1]	J. Longino PC; Pennington 1981
	RUBIACEAE						
(N)	<i>Duroia</i> ^{U,pe}	I,y	Y,i ⁱ	(G?)H	Y	1(+)	Campbell et al. 1989; DD
<i>Petalomyrmex</i>	FABACEAE						

(E)	<i>Leonardoxa</i> ^{U,p}	I,n	N,y	E	Y	1	McKey 1984; 1991; Snelling 1979
Plagiolpidini							
<i>Plagiolopsis</i>	STERCULIACEAE						
(E)	<i>Cola</i> ^{SU,pe}	L,y	?,?	?	Y	1	Bq
Camponotini							
<i>Camponotus</i> (subgenus <i>Pseudocolobopsis</i>)							
	CECROPIACEAE						
(N)	<i>Cecropia</i> ^{TU,pg}	S,n	N,y	BPH	Y	2	DD
<i>Camponotus</i> (Oriental and Australian subgenera often referred to as <i>Colobopsis</i>)							
	BIGNONIACEAE						
(O)	<i>Stereospermum</i> ^{T,ε}	Sp,N	?,?	HE	N	[1]	DM; T. Musthak Ali PC
	FLACOURTIACEAE						
(A)	<i>mRyparosa</i> ^{T,p}	S,n	?,?	?	?	1	H&W
	RUBIACEAE						
(O)	<i>Myrmeconaucllea</i> ^{S,ε}	I,n	?,?	?	Y	[2]	Maschwitz & al. 1989
	RUTACEAE						
(O)	<i>Zanthoxylum</i> ^{U,ε}	S,y	?,?	?	Y	[1]	Maschwitz & Fiala 1992
	VERBENACEAE						
(O)	<i>Clerodendrum</i> ^{U,ε}	S,n	?,?	E	Y	1	J; Beccari 1884
<i>Camponotus</i> (other subgenera)							
	CECROPIACEAE						
(N)	<i>Cecropia</i> ^{T,εg}	S,n	N,y	BPH	Y	1	B; D
	EUPHORBIACEAE						
(A)	<i>Endospermum</i> ^{T,pe}	Sp,n	S,y	EW	Y	1	Bq; J; DD, Monteith 1987; Letourneau et. al. PC
(O)	<i>Macaranga</i> ^{T,es}	S,n	?,?	?	Y	2	Fiala & al. 1990; F. Rickson PC
	PALMAE						

(A)	<i>Drypetes</i> ^{2,3}	S,?	?,?	?	?	M. Jebb PC
(A)	<i>Glochidion</i> ^{U,3}	S,?	?,?	?	?	M. Jebb PC
(A)	<i>Homalanthus</i> ^{2,2}	S,?	?,?	?	?	M. Jebb PC
(N)	<i>Mabea</i> ^{2,2}	Sp,?	?,?	?	?	Spruce 1908
(A)	<i>Pinelodendron</i> ^{2,e}	S,?	?,?	?	?	M. Jebb PC
	FABACEAE					
(N)	<i>aTachigall</i> ^{U,p}	P,y	?,?	?	Y	DD
	GENTIANACEAE					
(N)	<i>Tachia</i> ^{SL,p}	S,n	?,?	E?	Y?	Bq; B; Spruce 1908; Maguire & Weaver 1975
	LAURACEAE					
(A or O)	<i>Cryptocarya</i> ^{2,2}	S,?	?,?	?	?	H&W
	LOGANIACEAE					
(O)	<i>Fagraea</i> ^{H,p}	P,n	?,?	?	?	J
	MELASTOMATACEAE					
(N)	<i>aAllomatieta</i> ^{S,2}	L?,y	?,?	?	?	A. Gentry PC
(N)	<i>Blakea</i> ^{2,2}	L?,y	?,?	?	?	B
(N)	<i>aHenriettea</i> ^{2,2}	L,y	?,?	?	Y	W. Judd PC; S. Renner PC; B; H
(O)	<i>Medinilla</i> ^{H,b}	L,y	?,?	P,?	Y	J; Solereder 1920
(N)	<i>Topobea</i> ^{2,2}	P,?	?,?	?	Y?	S. Renner PC
	MELIACEAE					
(A)	<i>Aglai</i> ^{U,p}	Sp,n	?,?	?	N	H&W
	MONIMIACEAE					
(A)	<i>Kibara</i> ^{U,p}	I,n	?,?	H	Y?	Bq; J; Philipson 1985
	NYCTAGINACEAE					
(O)	<i>Pisonia</i> ^{2,2}	S,y	?,?	?	?	H&W
	PALMAE					

(O)	[†] <i>Calamus</i> ^{R,p?}	Cl,y	?,?	?	N	?	Bq; J. Dransfield PC
(O)	[†] <i>Calamus</i> ^{R,?}	O,y	?,?	?	Y	?	J. Dransfield 1981
(A)	[†] <i>Calamus</i> ^{R,?}	O,y	?,?	?	Y	?	J. Dransfield 1981
(O)	[†] <i>Calamus</i> ^{R,?}	Ga,y	?,?	?	Y	?	Dransfield & Manokaran 1978
(E)	[†] <i>Eremospatha</i> ^{R,?}	Cl,y	?,?	?	Y	?	J. Dransfield PC
(E)	[†] <i>Laccosperma</i> ^{R,?}	O,y	?,?	?	Y	?	J. Dransfield PC
(E)	<i>Laccosperma</i> ^{R,?}	Ac,n	?,?	?	Y	?	J. Dransfield PC; Zizka & al. 1990
(O)	[†] <i>Pogonotium</i> ^{R,?}	A,y	?,?	?	Y	?	Dransfield 1979 & PC
	PIPERACEAE						
(O)	<i>Piper</i> ^{?,?}	L,y	?,?	?	Y?	?	J; de Candolle 1916
	RUBIACEAE						
(E)	<i>Bertiera</i> ^{St,u,p}	St,n	?,?	?	N	?	S&B
(E)	^p <i>Heinsia</i> ^{Sp}	l,n	?,?	H	Y	?	Bq; J
(A)	^q <i>Nauclea</i> ^{U,e}	S,n	?,?	?	N	?	M. Jebb PC
(A)	<i>Psychotria</i> ^{S,?}	St,?	?,?	H	?	?	Bq; Schumann & Lauterbach 1901
(E)	<i>Trichystia</i> ^{U,p}	Sp,n	?,?	H	N	?	Hallé 1970; Robbrecht 1979
(E)	<i>Vangueriopsis</i> ^{?,?}	l,?	?,?	?	?	?	S&B; H&W
	RUTACEAE						
(A)	<i>Zanthoxylum</i> ^{U,e}	S,n	??	?	Y?	?	Hartley 1966; Maschwitz & Fiala PC
	SAPINDACEAE						
(A)	<i>Harpullia</i> ^{U,p}	Sp,s	?,?	?	N	?	Leenhouts & Vente; 1982; M. Jebb PC
	SCROPHULARIACEAE						
(O)	<i>Wightia</i> ^{L,?}	Sp,?	?,?	?	?	?	J
	SIMAROUBACEAE						
(N)	<i>Picrolemma</i> ^{?,?}	?,?	?,?	?	?	?	B
	SYMPLOCACEAE						
(A)	<i>Symplocos</i> ^{U,p}	?,?	?,?	?	?	?	M. Jebb PC
	THYMELAEACEAE						

(O)	<i>Wikstroemia</i> ^{2,3}	?,?	?,?	?	?	J
	VERBENACEAE					
(O)	<i>Callicarpa</i> ^{U,x}	L,y	?,?	EG	Y	? van Steenis 1967; H&W

- a Habitats listed for *Tachigali* include forest light gaps. In these semelparous trees, gaps colonized are often those left by dead maternal parents.
- b Extrafloral nectaries well developed only on orthotropic axes (thus most abundant on seedlings and sucker shoots, found also at growing tip of trunk).
- c Includes *Paracryptoceras* (see Hölldobler and Wilson 1990).
- d Includes *Microphysca* (Judd and Skean 1991).
- e Includes *Myrmidone* (Judd and Skean 1991).
- f The indumentum of these rattans is composed of spines of varying size and density; the scattered, triangular spines of some *Kortalsia* species probably do not inhibit ant movements, as in other hairy ant-plants. They may prevent vertebrates from opening domatia to feed on ant brood (see text).
- g Some *Pheidole* spp. use carton to construct nests or shelters, but use of carton is not as elaborate in this genus as in *Crematogaster* or *Azteca*.
- h *Anthobembix hospitans* (Becc.) Perkins, cited by Bequaert (1922) is a synonym of *Stegantthera hospitans* (Becc.) Kan. & Hat., cited by Hölldobler and Wilson (1990) (Philipson 1984).
- i Ants create "trail systems" by cutting trichomes on stems and domatia.
- j Includes *Ossaea* p.p. (Judd 1989; Judd and Skean 1991).
- k Includes *Pterocladon sprucei* Hook. f. ex Cogn. (synonymous with *Miconia bailloniana* Macbr.: S. Renner, personal communication) of Forel 1904.
- l Pattern of host fidelity is complex in this case, which involves supay chacras (see text).
- m *Gertrudia* (*G. amplifolia*) of Bequaert [1922] and Hölldobler and Wilson [1990] is a synonym of *Ryparosa* (Mabberley 1987).
- n A cloud-forest shrub of Colombia, *Allonaieta* resembles *Maieta* but has poorly developed or (on occasion) no domatia.
- o Myrmecophytism is included in *Henriettella*, which Judd and Skean (1991) now place in *Henriettea*.
- p "*Sina spininoda* Andr." (= *Tetraponera aethiops* [F. Smith], Pseudomyrmecinae) was recorded by Stütz (1910, 1913) from "*Epitaberna myrmecia* K. Schum." (= *Heinsia myrmecia* [K. Schum.] N. Halle). Herbarium material examined by Stütz (1910, 1913) from "*Epitaberna* intermodal swellings of this plant are too small to harbor this large ant, and we suspect this record is an error.
- q All Asian *Nanulea* listed by Bequaert (1922) and Hölldobler and Wilson (1990) are treated by Ridsdale (1978) as *Neonanulea* or *Myrmeconanulea*.

This work is dedicated to the memory of Alwyn Gentry, whose recent passing is a tragic loss to tropical biology.

**Archaeoscoliinae, an Extinct Subfamily of Scoliid Wasps
(Insecta: Vespida = Hymenoptera: Scoliidae)**

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Abstract.—Archaeoscoliinae, new subfamily, is established in the Scoliidae for three new fossil genera and four new species: *Archaeoscolia senilis*, *Cretoscolia promissiva*, *C. patiens*, and *Floriscoscolia relicta*, from the Aptian (Early Cretaceous) of Mongolia, Cenomanian (Late Cretaceous) of Northeast Siberia, Turonian (Late Cretaceous) of Kazakhstan, and Oligocene (mid-Tertiary) of Colorado, respectively.

INTRODUCTION

The Scoliidae is a rather small family of aculeate wasps belonging to the superfamily Scoliioidea (Rasnitsyn 1988) and embracing some 500 species (Brothers 1975). The fossil history of the family is little known. The only undisputable fossil representative, *Scolia prismatica* Smith, 1855, from the Miocene of Shandong, China (attributed by Zhang (1989) to a living species), as well as two doubtful ones, *Scolia? distincta* Zhang (1989), found with the above species, and *S. saussureana* Heer (1865), from the Upper Miocene of Oeningen, Germany, all belong to the Scoliinae, a cosmopolitan subfamily with greatest species diversity in warmer areas. The other subfamily, Proscoliinae, includes two species of a single relict genus, *Proscolia* Rasnitsyn (1977), from the eastern Mediterranean (Rasnitsyn 1977, Day et al. 1981, Osten 1987).

The above fossils represent only a small section of scoliid history. The Paleontological Institute, Russian Academy of Sciences, Moscow (further abbreviated as PIN), and the American Museum of Natural History (further referred to as AMNH) both have additional fossil material that extend the minimal age of the family well into the Cretaceous, and shed light on the early stages of scoliid evolution.

I would like to discuss two peripheral issues here. The first is my use of the ordinal name Vespida in the title instead of the traditional Hymenoptera. My reasons are explained in full elsewhere (Rasnitsyn (1982, 1988, 1989, 1992). In summary they represent, first, appreciation of the general superiority of typified names (i.e., based on a generic name) over descriptive ones in taxonomic

nomenclature. This is a simple extension of principles in use for superfamily-family names for nearly 250 years. The second reason is the developing awareness, at least among some Russian workers (e.g. Starobogatov 1991), that ordinal names should be based on established generic names. As to traditional names not based on generic ones, they seem useful and are used here in the form of vernacular names (e.g., hymenopterans, apocritans, etc.).

The second point concerns my approach to cladistics. I appreciate the advantages of cladistic methods in the study of phylogeny, and I do my best to follow them in that kind of research. I deviate from traditional cladistic taxonomy in one important respect: I consider paraphyletic (ancestral) taxa as fully legitimate (for details see Rasnitsyn 1987, 1988, 1992). This makes it possible to establish a new subfamily for the fossils in this paper, which represent a paraphyletic group.

DESCRIPTIONS

Archaeoscoliinae Rasnitsyn, new subfamily

Diagnosis.— Fore wing (Fig. 1) with outer veinless zone narrow and not corrugated. Unlike Proscoliinae, cell r long, cell 3r-m closed. Unlike Scoliinae, crossvein 2r-rs short, straight, crossveins r-m and 2m-cu always present. Hind wing (Figs. 3, 5) with RS and M very long before r-m, position of cu-a variable in respect to M-Cu fork. Head (Fig. 5) with clypeus short, antantennal tubercles weak, and, unlike Scoliinae, inner orbit only gently curved, oral cavity (Fig. 1) and, by implication, mouthparts

short. Scutum with notauli (Fig. 1, na) deep. Scutellum (Fig. 5, scl) elevated above metanotum (N3) instead of being leveled with it as in Scoliinae. Metanotum (Fig. 5, N3) short, clearly segregated in lateral depressions and central elevated area (metascutellum). Metasternal plate (Fig. 7, S3) small (though larger than largest in Tiphidae), separating widely both mesosternal lobes and midcoxae but apparently not hindcoxae. Unlike Scoliinae, male hypopygium lacking 3 long spines exerting from abdominal apex, otherwise its precise form unknown (Fig. 7). Unlike Proscoliinae, body size large (20-30 mm instead of 5.5-11.5 mm).

Taxonomic position and relationships.—The fossils under description are assigned to the Scoliidae based on the following scoliid synapomorphies. In the fore wing (Fig. 1), the pterostigma is narrow, with crossvein r-rs extending from its apex, and cell 2rm is about as long as cell 1mcu and produced basally to reach or even to surpass midlength of the upper side of 1mcu. In the thorax, the propodeal dorsum is longitudinally tripartite (known for *Archaeoscolia senilis*, Fig. 1), and the metasternal plate is widely separating the mesosternal lobes (known for *Floriscolia relict*a, Fig. 7, S3).

The venational characters are of particular importance, for unlike the other two characters listed above, they are present in all the fossils described here, including the incompletely preserved *Cretoscoliapatiens* (Fig. 5) which otherwise would hardly be identified as a member of the Scoliidae. On the other hand, unlike the structure of the propodeum and metasternal plate, the venational characters as described here are not uniquely derived. However, when taken in more detail, the character state of the cells 2rm and 1mcu widely overlapping each other can be considered as uniquely derived. Indeed, the same character state is known in bees (*Bombus* spp., *Xylcopa* spp., etc.), velvet ants (*Myrmosa* spp., *Pseudophotopsis* spp., etc.) and ants (many Ponerinae and Dolichoderinae). However, this overlapping is correlated in bees, ants, and velvet ants with, and probably achieved via, shortening of either 1mcu (in ants) or, in bees and velvet ants, 1+2r (the first submarginal cell). In contrast to these groups but similar to the living scoliids, the fossils under description retained both

1+2r and 1mcu cells long. Combined with the elongated basal half of the 2rm cell, this indicates that in both living and fossil Scoliidae the cells are widely overlapping due to direct elongation of the 2rm cell between the otherwise not modified 1+2r and, 1mcu cells.

Within the family the fossils display several important autplesiomorphies: head with the adantennal tubercle small (known for *Cretoscoliapatiens*, Fig. 5, at), thorax with the metasternum small (known for *Floriscolia relict*a, Fig. 7, S3), and fore wing with the outer, veinless zone narrow and smooth, not corrugated (also known for *Floriscolia relict*a, Fig. 7). The fossils lack synapomorphies that would permit assigning them to either of the two extant scoliid subfamilies.

Archaeoscolia Rasnitsyn, new genus

Diagnosis.—Apex of cell r just at crossvein 3r-m. Cell 3rm hardly elongate. Legs short, robust.

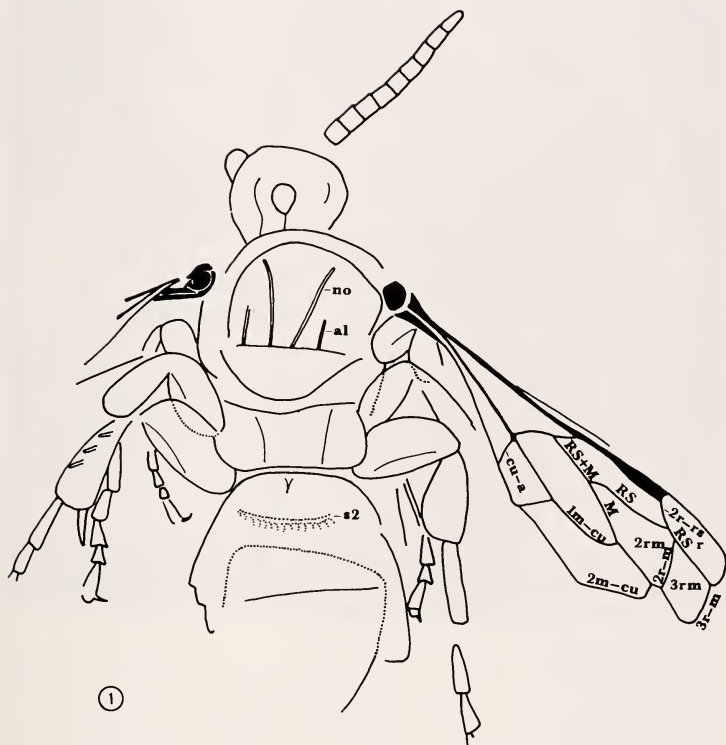
Type species.—*A. senilis*, new species, from the later Early Cretaceous of Central Mongolia.

Etymology.—The generic name is feminine, combined from the Greek adjective *archaios* meaning old, and the generic name *Scolia*.

Archaeoscolia senilis Rasnitsyn, new species (Figs. 1, 2)

Description.—Sex not definitely known, but judging from general appearance is female. Body length minimum 20 mm, fore wing length up to end of cell 3rm 15 mm. Antenna not coiled, gradually becoming more narrow distally, with first segment preserved (true second or third) quadrate and last one twice as long as wide, flagellomeres subequal in length except last three longer. Fore wing with cell r obliquely truncate at junction with 3r-m, crossveins 2-3r-m both oblique, subparallel, 2r-m close to 2r-rs, cell 3rm rhomboid, cu-a scarcely postfurcal. Legs short, stout, hind tibia with long, stout spines on outer surface. No coarse surface structure discernible except reticulation on central propodeal area and short longitudinal ribs beyond reflexed anterior rib of second metasomal sternum. Ground color of body and appendages dark.

Holotype.—Unique specimen PIN #3359/4524 collected 5 to 8 km North of Bon Tsagaan Nuur



Figs. 1. *Archaeoscolia senilis*, new species, dorsal view. Scale line here and elsewhere 10 mm. Dotted lines represent structures seen through overlaying ones. Abbreviations: 2rm, 1mcu, r, etc. = cells; 2r-rs, 3r-m, 1m-cu, etc. = crossveins; no = notaulus; S2 = anterior rim of 2nd metasomal sternum.



Figs. 2. *Archaeoscolia senilis*, new species.

Lake, Bayanhongor Aymag (Region) in Central Mongolia, in upper Lower Cretaceous deposits probably of Aptian age.

Etymology.—The species name is the Latin adjective *senilis* meaning old.

***Cretoscolia* Rasnitsyn, new genus**

Diagnosis.—Unlike *Archaeoscolia*, cell *r* apex distant from 3*r*-m, and legs comparatively long and

slender. Cell 3*rm* not elongate. Hind wing with *cu*-a beyond M-Cu fork.

Type species.—*C. promissiva*, new species, from the earlier Late Cretaceous of Northeast Siberia.

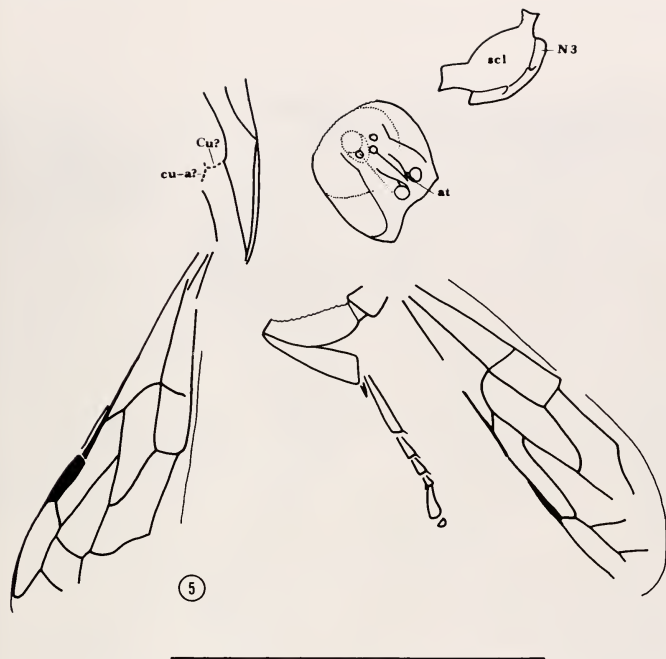
Etymology.—The generic name is feminine, a combination of the island name Crete (from which the scientific name of chalk and the Cretaceous period are also derived), and the generic name *Scolia*.



Figs. 3. *Cretoscolia promissiva*, new species, ventral view.



Figs. 4. *Cretoscolia promissiva*, new species.



Figs. 5. *Cretoscolia patiens*, new species. Abbreviations: at = adantennal tubercle; N3 = metanotum; scl = mesoscutellum.

***Cretoscolia promissiva* Rasnitsyn, new species**
(Figs. 3, 4)

Description.—Female. Body size probably ca. 30 mm fore wing length up to apex of cell r 12 mm. Fore wing with apex of cell r distant of wing margin, scarcely surpassing apex of cell 3rm, 3rm shorter than high, crossvein 2r-m oblique, 3r-m strongly bent outward, much closer to 2r-m on M than on RS, cu-a scarcely postfurcal. Hind wing with curved incomplete supernumerary r-m crossvein (possibly individual aberration), cu-a far

beyond M-Cu fork, Cu not bent at fork. Femora and tibiae narrow, hind tibia without evident spines on outer surface, hind tarsomere 5 thicker than hind tibia basally. Hind tibia with row of long, thick setae, hind tarsus covered with dense, thick, long setae, metasoma setose. Body and appendages probably dark.

Holotype.—Unique specimen PIN #3901/151 collected at Obeshchayushchiy Stream, right tributary of Nil River upstream in Arman' River basin, Magadan Region in Northeast Siberia, in lower Upper Cretaceous (Cenomanian) deposits of Ola



Figs. 6. *Cretoscolia patiens*, new species.

formation.

Etymology.—The species name is the feminine form of the Latin adjective *promissivus* meaning promising; this is the meaning of the Russian stream name *Obeshchayushchiy*, the type locality.

***Cretoscolia patiens* Rasnitsyn, new species**

Figures 5, 6

Diagnosis.—Unlike type species, apex of cell r

minimally distant from wing margin and far exceeding apex of cell 3r-m, crossvein 3r-m probably oblique and not strongly bent.

Description.—Sex unknown. Body size unknown, fore wing length ca. 11 mm. Ocelli in low triangle, with hind ones ca. 1.5 times closer to eye than to each other and ca. 1.5 times closer to median ocellus than to eye. Frons with strong elevated line running from mid ocellus to between antennal bases, and with sinuate impressions extending dor-

sad from adantennal tubercles. Occipital carina complete or almost complete. Back surface of head with long longitudinal line apparently representing combined intergenal and interpostgenal sutures and indicating oral cavity as short (posterior cephalic structures are shown in dotted lines at Fig. 5). Fore wing with cell apex minimally distant from wing margin and far exceeding apex of cell 3m, crossvein 2r-m close to 2r-rs, 3r-m as preserved oblique, subparallel to 2r-m (possibly bent in its posterior quarter), cell 3r-m rhomboid, cu-a interstitial. Hind wing without supernumerary r-m, Cu apparently strongly bent at fork, meeting cu-a just beyond fork. Leg moderately short, stout, probably with trochantellus delimited. Head dark, adantennal tubercles light, other fragments preserved (leg, metanotum, and obscure thoracic fragments) light except scutellum darker with light central area. No surface sculpture discernible.

Holotype.—Unique specimen PIN #2783/260 collected at Kzyl-Zhar Hill in the north part of Karatau Range, Chilli District of Kzyl-Orda Region in Kazakhstan, in lower Upper Cretaceous (Turonian) deposits.

Etymology.—The name is the Latin adjective patients, alluding to the poor state of the fossil.

Floriscolia Rasnitsyn, new genus

Diagnosis.—Fore wing with apex of cell r contiguous with wing margin, cell 3m much longer than high. Unlike *Cretoscolia* hind wing with cu-a before M-Cu fork, and legs short, stout, even in male.

Type species.—*F. relict*a, new species, from the Oligocene of western North America.

Etymology.—The genus name is feminine, combining part of the name of the type species locality, Florissant, with the generic name *Scolia*.

*Floriscolia relict*a Rasnitsyn, new species

(Fig. 7)

Description.—Male (judging from 13-segmented antenna). Body size 30 mm, fore wing length to apex of cell r 16 mm. Antenna with scape moderately short, pedicel short, ringlike,

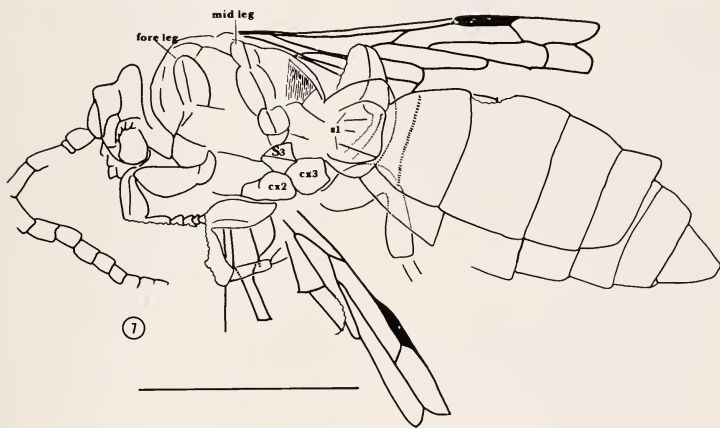


Fig. 7. *Floriscolia relict*a, new species, ventral view. Abbreviations: CX2, CX3 = mid and hind coxae; S1 = ist metasomal sternum; S3 = metasternal plate.

flagellomeres becoming shorter and somewhat narrower apically, first almost three times as long as wide, penultimate one subquadrate. Fore wing with crossvein 2r-m arching, subvertical, 3r-m strongly bent, cell 3rm almost twice as long as high, much longer on M than on RS. Hind wing cu-a meeting M+Cu shortly before fork, joining A in smooth curve. Legs very short, outer midtibial surface apparently without spines. Metasoma somewhat constricted between first and second segments, second sternum with transverse impressed line subbasally. Metasomal apex conical, with no signs of trispinose hypopygium. No surface sculpture found except fine vertical striation of propodeal sides. Body parts and appendages dark.

Holotype.—Unique specimen #28775 in AMNH collected at Florissant, Colorado, in deposits of Lower Oligocene (before mid-Tertiary).

Etymology.—The species name is the feminine form of the Latin adjective *relictus* meaning rest, alluding to the relict nature of the insect, which existed much later than its relatives.

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**A New Species of *Apocharips* from Costa Rica
(Hymenoptera: Cynipoidea, Charipidae)**

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Abstract.—*Apocharips hansonii*, new species, is described from Costa Rica. The wasp was reared from galls of Psyllidae. This is the first record of the genus *Apocharips* in the New World. Several unusual morphological features of the new species are discussed and illustrated.

Paul Hanson of the Universidad de Costa Rica reared a few specimens of a charipid from galls of the psyllid genus *Trioza* Förster that were collected at high elevations in Costa Rica. Charipids reared from Psyllidae belong in the subfamily Charipinae. Menke and Evenhuis (1991) recognized five genera of Charipidae with the subfamily Charipinae being represented by *Dilyta* Förster and *Apocharips* Fergusson. Hanson's material belongs to the last genus and establishes that *Apocharips* occurs in the Western Hemisphere. The specimens represent a new species.

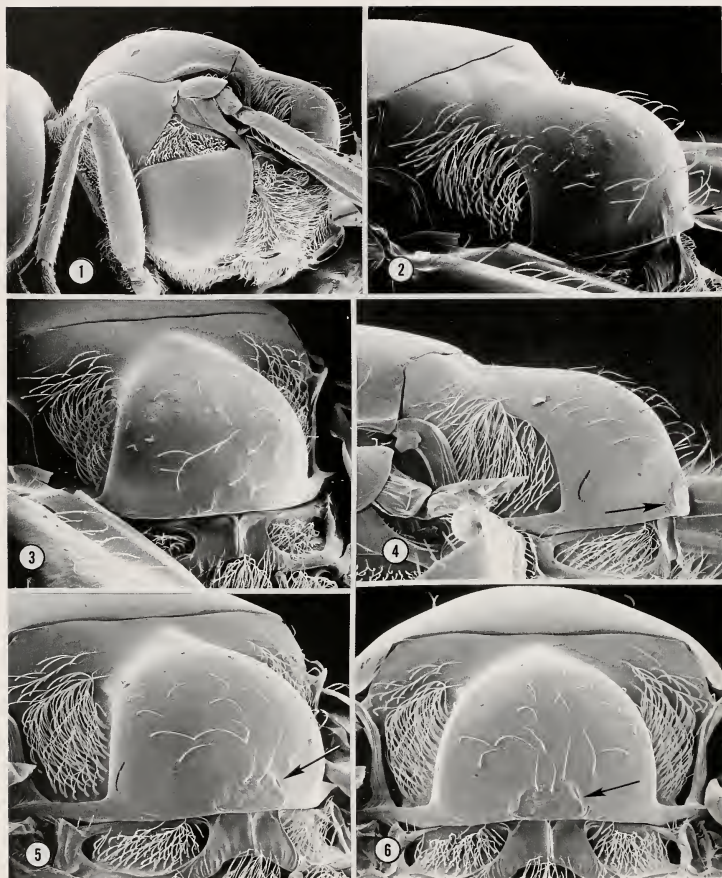
Carver (1993) recognized a sixth charipid genus, *Thoreanana* Girault, an Australian taxon that she removed from synonymy with *Alloxysta*, and assigned to Charipinae. *Thoreanana* has a small, basal tergum like *Apocharips*, but the antenna has 10-11 flagellomeres in the male and 9-10 in the female. All other genera of Charipidae have 12 male and 11 female flagellomeres.

The genus *Apocharips* was described by Fergusson (1986) for a European wasp now known by the name *trapezoidea* (Hartig) (see Evenhuis, 1982). Menke and Evenhuis (1991) listed four Old World species in the genus, all reared from Psyllidae. The new species is assigned to *Apocharips* because it has a small tergum 1 (Fig. 9) and the veins of the marginal cell reach the wing margin. However, unlike other members of the genus, the apex of the scutellum has an apical boss (Figs. 2-6) rather than a clearly formed M-shaped carina. Thus, in *Apocharips* the condition of the scutellar apex varies.

The presence of carinae at the apex of the scutellum was listed by Menke and Evenhuis (1991) as an autapomorphy of the subfamily Charipinae, but it is now clear that this character has limited value. Carver (1992) described and illustrated a new species, *Alloxysta carinata* (Alloxystinae), from Australia that has strong scutellar carinae apically. Thus at least one member of Alloxystinae has a character thought to be unique to Charipinae by Menke and Evenhuis. The new Costa Rican *Apocharips* described here further muddles the subfamily distinction since it only has a scutellar boss.

The new species has most of the other attributes of the subfamily listed by Menke and Evenhuis (1991, table 1), some of which are depicted here: two mandibular teeth (Fig. 11), no frontoclypeal sulcus (Fig. 11), and pronotum with lateral carina (Fig. 1). I did not check condition of the spiracles on tergum VI because of the small number of specimens available, but assume that they are narrowly separated as in other species of the genus.

The new species has another feature that is more intriguing than the condition of the scutellum. The face has converging ridges around the clypeus (Figs. 10-11). Such ridges appear to be unknown in any other member of the Charipidae, but are fairly common in the gall wasp family Cynipidae. This is evidently a parallelism.



Figs. 1-6. Male thorax features of *Apocharips hansonii*, specimens from Volcan Poás. 1, left side of thorax. 2, 3, posterolateral view of metanotum showing poorly defined apical boss (arrow). 4-6, left side, posterolateral, and rear views respectively, of metanotum showing more clearly defined apical boss (arrow).

***Apocharips hansonii* Menke, new species**

Black except as follows: scape and flagellomere I straw-colored; trochanters, apex of fore- and midfemora, foretibia, and foretarsomeres I-IV, straw-colored (midtibia and tarsus similar but darker). Face with numerous parallel ridges between eye and mandible base (Figs. 10-11). Flagellomeres I-IV of female antenna without linear tyli, but tyli present on V-XII; flagellomere II shorter than III, proportions of length of first three female flagellomeres: 6:3.5:4. Flagellomeres I-III of male antenna without tyli, but tyli present on remaining ones (Figs. 1-2); flagellomere I sinuate on outer side, longer than either II or III, proportions of flagellomeres I-III: 8:5.5:6. Apex of scutellum with a weak triangular boss that is not delimited by carinae (Figs. 2-3), or incompletely so (Figs. 4-6). Metanotum with median longitudinal carina (Figs. 3, 6). Vein stub from marginal cell as long as flagellomere II. Female 1.7 mm long, males 1.5-2 mm long.

Types.— Holotype female: Costa Rica, Cartago Prov., La Cangreja, 1950 m, March-May, 1992, Malaise trap operated by Paul Hanson (in National Museum of Natural History, Washington DC). Paratype males (four): one same data as holotype; two males, Alajuela Prov., Parque Nacional Volcan Poás, 2500 m, May 26, 1991, ex *Trioxa* sp. leaf gall on *Phoebe* or *Nectandra* (Lauraceae), collected by Paul Hanson; one male, same locality and host, Sept. 22, 1991, collected by Paul Hanson. Paratypes will be deposited in the Museo de Insectos, Universidad de Costa Rica, and the National Museum of Natural History.

Discussion.— *Apocharips hansonii* differs from the Old World species *trapezoidea* in a number of significant ways. *A. hansonii* has facial ridges that converge on the clypeus (Figs. 10-11), no tyli on the first three male flagellomeres (Fig. 7), a feeble triangular boss on the scutellum (Figs. 2-6), and a carina on the metanotum (Figs. 3, 6); these features immediately separate *hansonii* from *trapezoidea*. I have examined a single female of *trapezoidea* (Hartig), and the figures in the well illustrated description of *trapezoidea* by Kierych (1979). *A. trapezoidea* lacks facial ridges, the male has tyli on all flagellomeres, the scutellum has an M-shaped

carina apically, and the metanotum lacks a median carina. The head of *hansonii* in frontal view is more circular (Fig. 10) than that of *trapezoidea*. In the latter species the area below the eyes is more elongate and narrowed toward the mandibles. The spur on the marginal cell is longer in *hansonii*, particularly in the male.

Distribution.— Known only from elevations between 1950-2500 m in Costa Rica.

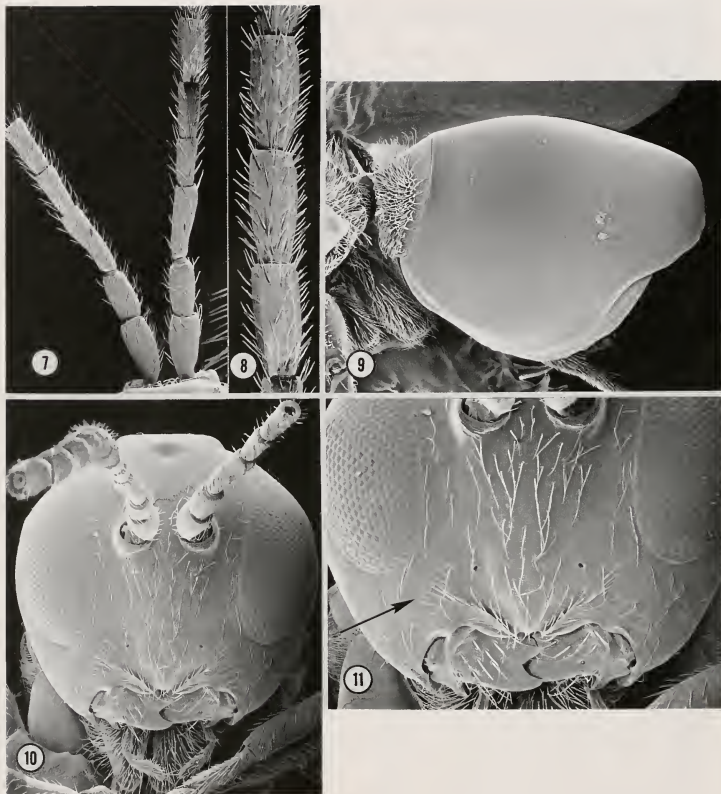
Etymology.— This tiny wasp is named after Paul Hanson who, by running many Malaise traps over a period of years, has probably sampled the micro-Hymenoptera fauna of Costa Rica more thoroughly than anyone else.

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Figs. 7-11. Male features of *Apocharips hansonii*. 7, dorsal view of scape, pedicel and flagellomeres 1-3 (and 4). 8, dorsal view of flagellomeres 4-6 enlarged from right antenna shown in fig. 7. 9, left side of abdomen. 10, 11, view of face, arrow points to facial ridges.

New Neurotoxins From Venoms Of Aculeate Hymenoptera: A Contribution To The Knowledge Of Stinging Behaviour

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Abstract - Several Hymenoptera produce a venom which contains a neurotoxic component. Kinins, present in venoms of vespid, scoliid, tiphiid, multilid and formicid Hymenoptera, irreversibly block the transmission in the insect CNS presynaptically by depletion. Poneratoxin, a neurotoxic compound isolated from ant venom, affects the ion current in voltage-dependent channels in nerve and muscle fibres. Philanthotoxins block the neuromuscular transmission and the synaptic transmission in the CNS of insects. The results support the idea that entomophagous Aculeata sting their prey in the CNS and explain the effects of the sting on insects and mammals.

INTRODUCTION

Within the phylum Arthropoda several groups include well known producers of venoms: the spiders, the scorpions and the hymenopteran insects. In the first seventy years of this century a number of arthropod venoms has been described. A manual of information was presented in a volume on Arthropod Venoms edited by Sergio Bettini (1978). The biochemical, pharmacological and behavioural aspects of venoms produced by Hymenoptera were collected together by Piek (1986). Although the latter book provides the reader with extensive documentation of observations and research during the last 100 years on bee, wasp and ant venoms, several of the most interesting wasp and ant neurotoxins which have a relation to the stinging behaviour of these insects were not yet chemically characterized in the first half of the 1980's. It is the aim of this paper to review the several types of neurotoxic effects of solitary wasps and thus contribute to the understanding of stinging behaviour.

HYMENOPTERA AS NEUROTOXIN PRODUCERS

The earliest report of a neurotoxic effect on an insect by a solitary wasp may be in the Erh-ya yin t'u or Dictionary of Old Terms, of which the Sung illustrations may originate between 500 and 400 BC (Bodenheimer 1928). The idea, that "in seven days the worm stung by the wasp was transformed

into the son of the wasp," conveys the notion that the prey was not killed but was otherwise incapacitated.

A principal question during the eighteenth and nineteenth centuries was whether prey of solitary aculeate wasps were killed or paralysed. Advocates of the killing idea were Réaumur (1742) and Dufour (1841). Sympathizers with the idea that prey of solitary wasps were not killed but paralysed were, for example, Bartram (1744, 1749) and Audouin (1839). It fell to Fabre (1855) to settle the conflict of views by electrically stimulating weevils, stung to a complete and irreversible immobility by the sphecid wasp *Cerceris tuberculata* (Villers) thus demonstrating that the prey was capable of movement and therefore in deep paralysis, not dead.

Solitary wasp venoms cause paralysis by neurotoxic action and we now know that neurotoxic principles are also found in bee venoms, social wasp venoms and ant venoms.

KININS FROM VESPID AND SCOLIID WASP VENOMS

Kinins are neurotoxic components of wasp and ant venoms, causing in the insect central nervous system a presynaptic block of the cholinergic transmission by means of an irreversible depletion of transmitter substance (acetylcholine), probably by means of a non-competitive inhibition of the presynaptic choline-uptake (Piek et al. 1987, 1990; Piek 1991).

Wasp kinins are polypeptides of 9-18 amino acid residues containing a bradykinin-like sequence as part of the molecule. The bradykinin-like sequence is either identical to the vertebrate bradykinin, or differs in a single OH-group (prolin becomes hydroxyprolin, Hyp^3 -bradykinin) or differs in a single CH_3 -group (Thr^6 -bradykinin). A bradykinin-like substance was discovered as a venom constituent of the wasp *Paravespula vulgaris* (L.) (Jacques and Schachter, 1954) and was called wasp kinin (Schachter and Tain 1954). Although the chemical characterization of this wasp kinin is still unknown, other social wasp kinins have been characterized chemically (for reviews see Nakajima 1986 and Piek 1991).

Despite the fact that wasp kinins have been known for more than 35 years, their neurotoxic actions had not been discovered before the demonstration of the presence of kinins in the venom of the solitary wasp *Megascolia flavifrons* (F.) (Piek et al. 1983, 1984b, Yasuhara et al. 1987). A point of interest is that this wasp stings larvae of the European rhinoceros beetle *Oryctes nasicornis* L. producing an irreversible paralysis, by successively penetrating the ventral side of all segments, which contain nerve ganglia (Piek et al. 1983). This scoliid wasp probably injects its venom into the nerve ganglia, a phenomenon which has commonly been observed for many solitary aculeate wasps (see also section on philanthotoxins). The idea that these wasps sting into the nerve ganglia prompted study of the effect of the venom and its fractions, and of purified or synthesized toxins, by means of microperfusion of an insect ganglion. This became the start of a series of experiments on the neurotoxic action of threonine-6-bradykinin (Thr^6BK), the most active kinin in the venom of *M. flavifrons* (Yasuhara et al. 1987) and of *Colpa interrupta* (F.) (Piek et al. 1990).

When a venom solution, prepared of isolated venom reservoirs of *M. flavifrons* was injected into the haemolymph of an *Oryctes nasicornis* larva, or when a female *M. flavifrons* was forced to sting the larva, no paralysis occurred (Piek et al. 1983). However, the venom preparation was very active, as a blocker of synaptic transmission, when injected (by microperfusion) into the sixth abdominal ganglion of the cockroach, *Periplaneta americana* L. (Piek

et al. 1987). It was shown that Thr^6BK irreversibly blocks synaptic transmission from the cercal nerve XI of the cockroach to a giant interneuron in the sixth abdominal ganglion (Hue and Piek 1988, 1989).

The presence of kinins as producers of neurotoxic insecticidal effects in the venoms of Vespidae, Scoliidae, Tiphidae, Mutillidae and Formicidae might be resolved as a toxicological argument for the phylogenetic relationship of these groups (Piek 1991, 1992). However, part of this view is in conflict with other evidence (Brothers 1975).

PONERATOXIN, A NEUROTOXIC ANT VENOM COMPONENT

Compared to the information available for bee and wasp venoms, knowledge about neurotoxic ant venoms is limited. Nevertheless, ant venoms have provided new tools for the study of neurophysiology, such as piperidine alkaloids in fire ant venoms (review: Schmidt 1986) and poneratoxin (Piek et al. 1991 a,b).

Following envenomation of man by the ponerine ant *Paraponera clavata* (F.), Schmidt et al. (1984) reported uncontrollable trembling which was not caused by pain alone. The venom contains at least two fractions which block specifically neuronal signals in the insect central nervous system (CNS) (Piek et al. 1991a). One of the fractions of the crude venom was pharmacologically characterized as a kinin. Although the chemical structure of this ant kinin is still unknown, its pharmacological action is comparable to the wasp kinins described in the preceding section.

The second neurotoxic fraction proved to be the most potent blocker of CNS functions. It contained a very potent neurotoxic peptide of 25 amino acid residues, called poneratoxin (Piek et al. 1991a). This has been synthesized by Professor Terumi Nakajima (Tokyo). At concentrations varying from 10^{-8} to 10^{-6}M the synthetic poneratoxin (PoTX) blocks synaptic transmission in the insect CNS in a concentration-dependent way and it depolarizes giant interneurons. At comparable concentrations PoTX affects the electrical activity of isolated cockroach axons, as well as of isolated frog and rat skeletal muscle fibres. The explanation of these

actions is the finding that PoTX prolongs action potentials and thus induces slow automatic activity. This is a consequence of a slow sodium ion-current activation at unusual negative values of potential and due to slow deactivation (Piek et al. 1991b Duval et al. 1991, 1992). This explains the insecticidal action of a sting of the ant into an insect prey, and also the fibrillation of skeletal muscles of man (Schmidt et al. 1980) and insects (Piek et al. 1991b).

As a venom reservoir of a single ant specimen (*P. clavata*) may contain about 1 µg poneratoxin (Piek et al. 1991a), injection of its content may result, for small insects, in a final concentration of between 10^{-5} and 10^{-4} M. Even a tenth of the venom reservoir content injected into the CNS immediately and irreversibly blocks neuronal functions. For vertebrates about 30 stings of *Paraponera clavata* per kg can be lethal (LD_{50} : 33 stings/kg; Schmidt et al. 1980). If this results in about 30 µg of poneratoxin per kg, the final concentration of poneratoxin will be in the order of 10^{-6} – 10^{-7} M, a level which is probably lethal. The uncontrollable trembling and unbearable pain caused by a sting by *P. clavata* is explained by the hyperactivity of the nervous network caused by prolongation of action potentials.

It is concluded that poneratoxin alone could explain the reversible neurotoxicity of the venom of *P. clavata*, but the kinin present in the venom, may contribute to the insecticidal action considerably by blocking irreversibly the synaptic neurotransmission.

PARALYSIS OF PREY BY PHILANTHOTOXINS

The two first examples of neurotoxins (kinins and poneratoxin) are polypeptides produced by vespoid Hymenoptera. Our knowledge of venoms of those wasps which belong to a quite different group, the Apoidea spheciformes (or sphecid wasps) is relatively poor. The venom and its constituent neurotoxins has been well described for only a single species, i.e. that of the sphecid wasp *Philanthus triangulum* (F.). The venom contains at least two different toxins that are antagonists for the glutamatergic neuromuscular transmission in insects (Piek and Spanjer 1986). The two toxins are chemically characterized as β -philanthotoxin (β -

PTX) and α -philanthotoxin (PTX-4.3.3) respectively (Karst et al. 1990, 1991, Karst and Piek, 1991). These philanthotoxins are polyamine-like structures that block both the insect neuromuscular transmission and the nicotinic synaptic transmission in the insect central nervous system (Hue and Piek 1989, Karst et al. 1990, 1991, Karst and Piek 1991).

STINGING BEHAVIOUR

In his *Souvenirs Entomologiques* Fabre (1879-1910) presented the view that solitary wasps sting their victims in the CNS. He observed prey having a concentrated CNS (buprestid beetles, weevils and some beetle larvae) to be stung once and observed that prey with a more diffuse CNS were stung more than once. Among his examples were *Sphex* spp. which sting crickets three times, once in each of the three main nerve ganglia, and *Ammophila* spp. which sting caterpillars in every segment containing a major nerve ganglion.

Based on observations over more than twenty years, Steiner (1986) tested in sphecid wasps six different hypotheses concerning sting number, location of sting, sting direction and other characteristics. Conceivably, the number, location and direction of successive stings could have been affected by (1) soft spots in the integument of the prey (Ferton's soft spots hypothesis; Steiner 1986), (2) body segmentation, (3) leg bases, (4) complete set of ganglia or (5) ganglia involved in locomotion and defence. The null hypothesis would be random stinging. Steiner (1986) concluded that although a wide spectrum of stinging methods could not easily be encapsulated in a single simple formula, the locomotor ganglia hypothesis of stinging is the best-fitting one for a number of aculeate wasps which prey on large or powerful insects. These wasps give at least one different sting for each clearly separate nerve centre involved in locomotion, attack, defence or resistance of the prey.

In a single case the localization in a cross section of the mesothorax of *Musca domestica* L. of radioactively labelled venom of the sphecid wasp *Mellinus arvensis* L. has been demonstrated (Piek 1978, see also Steiner 1986). The extensive documentation on stinging behaviour in relation to the

effects of stinging on prey (Steiner 1986, Piek and Spanjer 1986) suggests a general rule: entomophagous Aculeata sting into the CNS of the prey. The blocking action in the insect CNS of the venoms of *Philanthus triangulum* (Hue and Piek 1989) and of *Megascolia flavifrons* (Piek et al. 1987) also supports Steiner's conclusion.

Several unpublished pilot studies in our laboratories indicate that the venoms of sphecids wasps other than *P. triangulum* did not affect the insect neuromuscular transmission. We may speculate that the ability of *P. triangulum* to paralyse its prey (workers of the honeybee) by a peripheral effect on muscle contraction has been developed because of the dangerous defensive behaviour of the prey. When, for example, a female *P. triangulum* is brought together with ten honeybee workers, the wasp is sometimes killed by one of the last bees to be attacked. Therefore, it may be safer for the wasp to give a random sting, which quickly but reversibly incapacitates the bee. Subsequently a sting is given into the thoracic ganglion complex and the process is often completed by a sting into the suboesophageal ganglion. This complete stinging sequence results in a long-term paralysis.

A different, but to a certain degree comparable stinging behaviour has been described for *Ampulex compressa* F. and *Liris nigra* F. A sting in the thorax of the cockroach transiently paralyses the victim. During that short-lived immobility of the cockroach, the wasp stings carefully into the suboesophageal ganglion. Only this latter sting results in a delayed and irreversible change of behaviour of the cockroach (Steiner, 1986, Piek et al., 1984, 1989).

It might be clear that the explanation of the atypical venom composition of *P. triangulum* has to be supported by studies of venoms of other bee-hunting or wasp-hunting sphecids wasps. It may be a challenge to students of the biology of the solitary wasps to collect arguments in favour or against the above mentioned view.

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**Syntomopus Walker: The Nearctic Species with a Review of
Known Host Associations (Hymenoptera: Pteromalidae)**

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Abstract.—*Syntomopus* Walker is a cosmopolitan genus of 13 described species. *Syntomopus* is defined, its relations to other pteromalid genera are discussed and a host list is presented for the species. Known hosts include mostly stem-mining Agromyzidae, but stem-mining Lepidoptera, and possibly Cynipidae are also hosts. The species of the United States and Canada are reviewed. *Syntomopus affinis* Ashmead, 1896 is synonymized with *S. americanus* Ashmead, 1894 and a new Nearctic species, *S. arpedes*, n. sp., is described.

Syntomopus Walker contains 13 described species: *S. shakespearei* (Girault), 1913 from the Australian region; *S. agromyzae* Hedqvist, 1972, *S. incisus* Thomson, 1878, *S. incurvus* Walker, 1833, *S. oviceps* Thomson, 1878, *S. pallipes* Rudow, 1886, and *S. thoracicus* Walker, 1833 from the Palearctic region; *S. fuscipes* Huang, 1991 from the Oriental region; *S. gracilis* De Santis, 1976 (in De Santis et al., 1976), *S. incidoideus* Howard, 1896, and *S. parsii* De Santis, 1976 from the Neotropical region; and *S. affinis* Ashmead, 1896 and *S. americanus* Ashmead, 1894 from the Nearctic region. In this paper, I synonymize *S. affinis* with *S. americanus* and describe a new Nearctic species, *S. arpedes*, n. sp.

Terminology in this paper follows that of Graham (1969), except that genal concavity is used instead of genal hollow and club is used instead of clava. In addition, the gastral terga are numbered T1–T7 beginning with the first tergite after the petiole. The following abbreviations are used: the median ocellar diameter is MOD, the ocellar–ocular distance is OOL, the posterior ocellar distance is POL, the lateral ocellar distance is LOL, the multiporous plate sensilla are MPP sensilla, the lower ocular line is LOCL, and the antennal funicular segments are F1 through F6. The units of measurement given in the descriptions can be converted to millimeters by multiplying by 0.02. The acronyms for the museums from which specimens were examined are given in the Acknowledgments.

Genus *Syntomopus* Walker

Syntomopus Walker, 1833:371, 372. (Type species: *Syntomopus thoracicus* Walker, 1833; sub. desig. by Westwood, 1839:69; examined). Förster, 1856:52, 56. Thomson, 1878:17, 23. Ashmead, 1904:330, 331. Schmiedeknecht, 1909:374, 375, 376–377. Nikol'skaya, 1963:247–248. Peck, Bouček, and Hoffer, 1964:40. Graham, 1969:124, 137–140. Hedqvist, 1972:210–215. Dzhanokmen, 1978:76, 79–80. Burks, 1979:787. Bouček, 1988:238, 466.

Merismorella Girault, 1926:1. (Type species: *Merismorella shakespearei* Girault; monotypy; not seen). Bouček, 1988: 466 (synonymy).

Description.— Head, mesosoma, coxae, petiole, gaster metallic dark blue or green; scape metallic or nonmetallic. Head with clypeus having three broad symmetrically arranged clypeal denticles (Fig. 1); lateral part of mouth margin with short genal concavity; antennal torulus distinctly above LOCL. Antenna with scape cylindrical, 5X as long as wide; flagellum compact, with segments cylindrical and typically transverse in females (quadrate in *S. agromyzae*); MPP sensilla in single row; club of female without large patch of micropilosity, tip lacking spine. Maxilla of male with palp slender, stipites unenlarged. Mesosoma flattened dorsally (Fig. 2) except in *S. agromyzae*; pronotal collar long, length 1/4–1/3 its width, dorsal level of collar below that of vertex, humeral angles squared, anterior edge rounded; notaulus shallow; scutellum

typically about as long as wide (longer than wide in *S. agromyzae*), lacking anterior median groove, with two pairs of lateral setae, frenal area nearly indistinguishable from remainder of scutellum; dorsellum crescent-shaped; propodeum with median panels long (width about 1.5X length), median carina (except in *S. incisus*) and plicae well developed and connected posteriorly by W-shaped carina. Fore wing with relative lengths of veins as follows: submarginal > marginal > postmarginal > stigmal; costal cell with at least one complete row of setae; basal cell bare; basal vein setose or bare; speculum developed, open posteriorly. Petiole longer than wide, cylindrical; with complete basal flange continuous laterally and ventrally; without median carina; lateral setae present. Gaster of female ovate acuminate; hypopygium extending to near tip of T7; in both sexes hind margin of T1 sinuous laterally, typically emarginate medially (entire in *S. oviceps*).

Discussion.—Finding a suite of character states to define *Syntomopus* is complicated by intermediate forms between it and *Thinodytes* Graham, *Mauleus* Graham, and *Ploskana* Bouček. The most distinctive characteristic of most *Syntomopus* species is the flattened mesosoma (Fig. 2), but this character state is of limited value for defining the genus. Flattened thoraces, similar to those of most *Syntomopus* species, occur throughout the Pteromalidae in many genera including *Ploskana*, *Ksenoplata* Bouček, and *Anogmus* Förster. Some *Syntomopus* species, such as *S. agromyzae* and some undescribed Neotropical species, have a normally arched mesosoma. As noted by Bouček (1988), the pronotal collar of *Syntomopus* is large, being 1/4 to 1/3 as long as wide and rectangular in dorsal view (Fig. 2). The pronotum of *Ploskana* is similarly lengthened, but it is distinctly narrowing anteriorly (see fig. 3, Bouček 1976). Besides having the character states defining the *Halticoptera*-group [those miscogasterine genera characterized by a reticulately sculptured body, acarinate pronotal collar, weakly developed notauli, weakly delimited frenum, propodeum with sharp median carina and plicae connected posteriorly by W-shaped carina, petiole with a basal bracing consisting of an anteriorly directed lateral and ventral flange, and the hind

margin of the first gastral tergum being sinuous laterally and usually emarginate medially; Heydon 1988], *Syntomopus* can be defined relative to other related genera by possession of the following two autapomorphies: 1—three symmetrically arranged clypeal denticles (Fig. 1) and 2—an enlarged pronotal collar with squared humeral angles (Fig. 2). Genera of related groups such as the *Cyrtogaster*-group (Heydon 1989) and *Nodisoplata* Graham also have three symmetrically arranged clypeal denticles, but this symmetrical arrangement of clypeal denticles is unique for *Syntomopus* within the *Halticoptera*-group.

Graham (1969) placed *Syntomopus* as the closest relative of *Sphegigaster* Spinola. This relation was echoed by Bouček (1976) in his description of *Ploskana*, which he described as having similarities to both of the former two genera. However, a close relationship between *Syntomopus* and *Sphegigaster* is unlikely since there are no synapomorphies supporting such a relationship between them. Character states they share in common are either plesiomorphic, such as the rounded anterior edge of the pronotal collar, or synapomorphies both *Sphegigaster* and *Syntomopus* also share with the other genera of the *Halticoptera*-group, such as the shallow notauli, short postmarginal vein, obliterated frenal sulcus, long reticulate petiole, and sinuous lateral margin of T1. *Sphegigaster* lacks character states that define the *Halticoptera*-group such as the W-shaped carina connecting the median carina and plicae, and the median emargination of the first gastral tergum. In *Sphegigaster*, species lack all traces of propodeal carinae, and the hind margin of T1 is entire mesally.

Biology.—*Syntomopus* is exceptional among the Pteromalidae because hosts are known for many of the described species (Table 1). *Syntomopus* species are parasitoids, emerging from the pupal stadium of insects boring the stems of plants—commonly Asteraceae. Their hosts are mostly Diptera, but *S. arpedes*, *S. americanus*, and *S. incurvus* have been reared from lepidopteran stem borers, and *S. incisus* has been reared from a cynipid gall.

From the illustration, it is clear that the two pteromalid parasitoids identified as *Syntomopus*

Table I. Hosts of *Syntomopus* species.

<i>Syntomopus</i> species	Insect Host	Plant Host	Literature citation
<i>Syntomopus agromyzae</i>	<i>Hexomyza cecidogena</i> (Hering) (Diptera: Agromyzidae)	twig galls on <i>Salix caprea</i> L. (Salicaceae)	Hedqvist 1972
<i>Syntomopus americanus</i>	<i>Agromyza</i> sp. (Diptera: Agromyzidae)	<i>Ambrosia trifida</i> L. (Asteraceae)	Webster 1894
	<i>Hexomyza schineri</i> Giraud	<i>Populus tremula tremuloides</i> (Michaux)	
	? <i>H. schineri</i> Giraud	<i>Populus alba</i> L.	
	? <i>Melanagromyza hicksi</i> Steyskal (Diptera: Agromyzidae)	<i>Althaea rosae</i> L. (Malvaceae)	Hansberry 1940
	<i>M. martini</i> Spencer		
	<i>M. virens</i> Loew	<i>Parthenium argentatum</i> Gray (Asteraceae)	Lange 1944 Cassidy et al. 1950
	<i>Phalonia voxcana</i> Kft. (Lepidoptera: Cochylidae)	stems of <i>Prenanthes alba</i> L. (Cichorieae)	
	<i>Phytomyza flavicornis</i> Fallén (Diptera: Agromyzidae)		
<i>Syntomopus arpedes</i>	<i>Epiblema strenuana</i> (Walker) (Lepidoptera: Tortricidae)	<i>Ambrosia</i> sp. (Asteraceae)	
<i>Syntomopus incisus</i>	<i>Melanagromyza lappae</i> (Loew)	<i>Arcium vulgare</i> (Hill) Evans (Asteraceae)	Graham 1969
	<i>M. aenovenstris</i> (Fallén)	<i>Cirisium eriophorum</i> (L.) Scopoli (Asteraceae)	Graham 1969
	<i>M. dettimeri</i> Hering	stems of <i>C. eriophorum</i>	Graham 1969
	<i>Phanacis hypochaerides</i> (Kieffer) (Hymenoptera: Cynipidae)	<i>Hypochoeris radicata</i> L. (Asteraceae)	Askew 1970

Table I. Hosts of *Syntomopus* species (continued).

<i>Syntomopus</i> species	Insect Host	Plant Host	Literature citation
<i>Syntomopus incurvus</i>	<i>Melanagromyza deitmeri</i> Hering <i>M. tripolii</i> Spencer <i>Adaina microdactyla</i> (Hübner) (Lepidoptera: Pterophoridae)		Graham 1969 Graham 1969 Askew 1970
<i>Syntomopus oviceps</i>	<i>Phytomyza flavicornis</i> Fallén (Diptera: Agromyzidae) stem borer	<i>Urtica dioica</i> L. (Urticaceae)	Graham 1969
<i>Syntomopus parisii</i>	<i>Melanagromyza cunctanoides</i> Blanchard	<i>Helianthus annuus</i> L. (Asteraceae)	DeSantis et al. 1976
<i>Syntomopus shakespearei</i>	<i>Liriomyza helichrysi</i> Spencer (Diptera: Agromyzidae)		Boucek 1988
<i>Syntomopus thoracicus</i>	<i>Melanagromyza aeneiventris</i> (Fln.)	stems of <i>Senecio jacobaea</i> L. (Asteraceae)	Graham 1969
<i>Syntomopus</i> spp.	<i>M. eupatorii</i> Spencer		Graham 1969
	<i>M. sojae</i> Zehnter		Huang 1991
	<i>Melanagromyza sojae</i> Zehnter	on bean (Fagaceae)	Kamijo 1983
	<i>M. tomatarum</i> Steyskal		Havránek 1987

species in Bruzon, Martinez, and Calderon (1968) are not *Syntomopus*.

***Syntomopus arpedes* Heydon, new species**

Figs. 2, 3

Holotype, female.— Color: Anterior of head, dorsum of mesosoma dark green, face and scutellum more blue; occiput, neck, pleural regions, coxae, petiole dark blue; gaster dark brown with metallic reflections on T1. Antenna with scape and pedicel yellow-brown with strong metallic green reflections; remainder brown. Legs with trochanters and femora brown with strong green reflections; tibiae yellowish brown mesally, paler at tips; fore tarsus yellow-brown; middle and hind tarsi white. Wing veins pale yellow-brown, parastigma more reddish brown.

Sculpture.— Clypeus smooth with fine striae laterally; frenum coriaceous; dorsellum smooth; T1–6 smooth; T7 coriaceous.

Structure.—Body length 2.3 mm. Head ovate in anterior view; width 1.2X height (36.5:31.0), 2.8X length (36.5:13.0) (Fig. 3); front of head flat, scrobes absent; lateral teeth of clypeus very weak; genal concavity extending 1/3 malar distance; eye height 2.1X length (19:9), 2.4X malar distance (19:8), length 3.0X temple length (9:3); ratio of MOD, OOL, POL, LOL as 3:6:9:4; torulus 1X own diameter above LOCL. Antenna with length of pedicel

plus flagellum 0.79X head width (29.0:36.5); ratio of lengths of scape, pedicel, annelli, F1–6, club as 11.0:4.0:1.0:3.0:2.5:2.5:2.5:2.5:8.0; widths of F1, F6, club as 3:4:4; club with patch of micropilosity ventrally on terminal segment. Mesosoma flattened dorsally (Fig. 2), length 1.9X width (60.0:31.5), width 2.1X height (31.5:15.0); pronotum with sides weakly convergent anteriorly, humeral angles squared, length 0.35X width (9.5:27.0); propodeum in same plane as rest of mesosoma, median carina complete but weakly developed, plicae sharp but fading out just at anterior margin of propodeum, nucha acarinate anteriorly. Fore wing length 2.2X width (85:39); ratio of lengths of submarginal, marginal, postmarginal, stigmal veins as 37:20:13:8; costal cell with single complete row of setae; basal cell with single seta in right wing, without seta in left wing; basal vein with four setae in left wing, two in right. Petiole length 1.6X width (12.5:8.0); with four pairs of lateral setae directed anteriolaterally. Gaster length 1.4X width (38:27); hind margin of T1 emarginate mesally; hypopygium extending to end of T7.

Allotype, male.— Color: Similar to holotype except all metallic areas dark blue. Structure: Body length 1.8 mm. Head width 2.4X length (31:13). Antenna with length of pedicel plus flagellum 1.1X head width (35:31); ratio of lengths of scape, pedicel, annelli, F1–6, club as 10.0:3.0:1.0:4.0:4.0:3.5:4.0:3.5:3.5:8.5; widths of F1, F6, club as 3:3:3; MPP



Figures 1-2. *Syntomopus* species. 1, *americanus*, female clypeus. 2, *arpedes*, female habitus.

sensilla short, extending less than 1/2 length of funicular segments, only one or two visible per segment at a time; flagellar pilosity dense, fine, semierect. Petiole length 1.8X width (11:6). Gaster length 1.1X width (20:18).

Variation.— The body color of the males varies from blue, like in the allotype, to green, like in the holotype. The body length of the females varies from 1.7 to 2.3 mm, and the body length of males varies from 1.8 to 2.1 mm. The ratio of head width divided by length averages $2.62 \pm (S.E.) 0.029$ ($n=11$, range=2.5–2.8) for females and 2.5 ± 0.023 ($n=8$, range=2.4–2.5) for males. Two of 12 females have setae on the basal vein and three of seven males do, but only one or two setae are usually present.

Discussion.— This species is similar to *S. americanus*, but the difference in the head shape, particularly of the females, is quite distinct (compare Figs. 3 & 4). The ratio of head width to length varies from 2.5–2.8 for females and 2.4–2.5 for males of *S. arpedes*, but from 2.2–2.4 for females and 2.1–2.4 for males of *S. americanus*. In addition, the vertex of *S. arpedes* females has a pinched appearance, while the vertex of *S. americanus* females is more evenly rounded anterioposteriorly. From the descriptions in De Santis et al. (1976), *S. arpedes* most closely resembles *S. parisii* in having the dorsum of the thorax very flat and the pronotum with the humeral angles squared. *S. arpedes* differs from *S. parisii* in having the scape metallic to the base and the side denticles of the clypeus much reduced compared to the central denticle. *S. parisii* has the scape yellow and the middle denticle of the clypeus only a little larger than the lateral denticles.

Type Material.— The holotype (USNM), allotype (USNM), and six female and three male

paratypes (CMNH, USNM) were reared from a Zinnia stem borer in September 1940 by R. M. Bohart in Westwood Hills, Los Angeles County, California. An additional 14 paratypes were collected as follows (INHS, UCDC, USNM): United States. ALABAMA: 1 ♀. CALIFORNIA: 5 mi w. Yuba City, 5 & 11.II.1971 [reared from *Xanthium strumarium* (Asteraceae)], 4 ♀, 2 ♂; Needles, 30.I.1977, 1 ♀; southern California, 11.IX.1950 (Zinnia plants), 1 ♂. ILLINOIS: University of Illinois South Farms (nr. Champaign), 27.VI.1981, 1 ♀. MARYLAND: Eldorado, 17.IX.1930 [ex. *Epiblema strenuana* infested *Ambrosia* (Asteraceae)], 1 ♀. TEXAS: Alpine, 30.VIII.1971 [*Happlopapus* (= *Machaeranthra*) *gracilis* (Asteraceae)], 1 ♀. México. NUEVO LEON: 9 mi s. Monterrey, 11.VIII.1972, 1 ♀; in car from Guaymas at Nogales, 22.IX.1950, 1 ♂.

Etymology.— The species name is from the Greek *arpedes*, meaning even or flat, and refers to the flat head of this species.

Biology.— The only determined host of *S. arpedes* is a tortricid lepidopteran, *Epiblema strenuana* (Walker) infesting *Ambrosia* (Asteraceae). *Syntomopus arpedes* has been reared in association with a number of Asteraceae, including Zinnia stem-borer material from Westwood Hills, California, *Xanthium strumarium* L. from near Yuba City, California, and from *Machaeranthra gracilis* (Nuttall) Shinnery in Texas.

***Syntomopus americanus* Ashmead**

Figs. 1 & 4

Syntomopus americanus Ashmead, 1894:51–52.

Webster, 1894:36. Dalla Torre, 1898: 167.



3



4

Figures 3–4. *Syntomopus* species. 3, *arpedes*, female head, dorsal view. 4, *americanus*, female head, dorsal view.

Nason, 1906:152. Schmiedeknecht, 1909:376. Girault, 1918:128. Glick, 1939:46. Hansberry, 1940:199, 711. Shread, Brigham, and Smith, 1941:495–496. Lange, 1944:394–395. Cassidy, Romney, Buchanan, and York, 1950:7. Peck, 1951:538. Peck, 1963:610. Burks, 1979:787.

Syntomopus affinis Ashmead, 1896:228, syn. n. Dalla Torre, 1898:167. Nason, 1906:152. Schmiedeknecht, 1909:376. Girault, 1918:128. Peck, 1951:538. Peck, 1963:609–610. Burks, 1979:787.

Ashmead (1896) gave the following differences between *S. americanus* and his new species *S. affinis*: 1. F1–5 elongate and F6 quadrate in *S. americanus*, while all the funicular segments transverse in *S. affinis*. 2. All the tibiae pale colored in *S. americanus*, while the middle and hind tibiae dark in *S. affinis*. 3. The median emargination of T1 deep in *S. americanus*, but running almost to the base of the first tergum in *S. affinis*. The type of *S. americanus* was misidentified as a female; however, and the differences listed above are those commonly found between males and females of a single common Nearctic *Syntomopus* species. The deeply cleft T1 must have been an error in observation because this state was not seen by me on the type or any other specimen of Nearctic *Syntomopus*. On the basis of my reexamination of the types of these two species and a comparison of the variation between the types and variation observed in other Nearctic *Syntomopus* material, I am synonymizing *S. affinis* with *S. americanus*.

Discussion.— Compared with the Palearctic *Syntomopus* species, *S. americanus* most closely resembles *S. incurvus* and *S. thoracicus*. Males of *S. americanus* differ from males of these Palearctic species by having the funiculus more slender, with all its segments, except sometimes F6, elongate. All the male funicular segments, except F1, are transverse in *S. thoracicus*, while F4–6 are transverse in *S. incurvus* (Graham 1969). *Syntomopus americanus* females differ from *S. incurvus* females by never having the anterior corners of the pronotum prominent and by having the stigmal vein shorter relative to the marginal vein. The length of the marginal vein averages $2.2 \pm (\text{S.E.}) = 0.023$ ($n=10$) times that of the stigmal vein in *S. americanus*, but varies

between 2.3 and 2.5 times in *S. incurvus*. Females of *S. americanus* have pale colored tibiae, not black like those of *S. thoracicus*. The ratio of head width divided by length averages $2.27 \pm (\text{S.E.}) = 0.025$ ($n=10$, range=2.2–2.4) for females and 2.27 ± 0.020 ($n=10$, range=2.1–2.4) for males of *S. americanus*.

Material examined.— *Syntomopus americanus* is among the most commonly collected species of miscogasterine pteromalids, and I examined 224 specimens from the following U.S. states and Canadian provinces and territories (ICCM, CNCI, FSCA, INHS, SEMC, UCDC, UCRC, USNM): Arizona, California, Colorado, Delaware, Florida, Illinois, Iowa, Idaho, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New York, Ohio, Oregon, Pennsylvania, South Carolina, Tennessee, Texas, Utah, Virginia, Washington, Alberta, British Columbia, Manitoba, Ontario, Quebec, Nova Scotia, Yukon Territory.

Biology.— *Syntomopus americanus* has been reared from a number of stem-mining Diptera, mostly Agromyzidae, but there is one record from a stem-boring cochylid lepidopteran. There is also a possible record from a cynipid gall on white poplar, but I believe that the gall of the poplar-galling agromyzid, *Hexomyza schineri* Giraud, was mistaken for a cynipid gall. The following is a list of host records from specimens examined: UNITED STATES. CALIFORNIA: Salinas, 20.X.1943, *Agromyza* (= *Melanagromyza*) *virens* Loew (Diptera: Agromyzidae) (USNM). DELAWARE: Newark, 6 & 7.V.1935, ragweed borer material (USNM). MICHIGAN: Gogebic Co., 15.V.1968, in gallery of *Saperda concolor* LeConte (Coleoptera: Cerambycidae) (USNM). NEW YORK: Ithaca, Winter 1925.1926, *Agromyza* (= *Melanagromyza*) *virens* (USNM); 21.II.1939, 6 & 15.III.1939, *Agromyza* (= *Melanagromyza*) *angelicae* Frost (Diptera: Agromyzidae) (USNM). OHIO: Eaton Mountain, 10 & 14.VI.1934, ex *Agromyza* (= *Melanagromyza*) *virens* (USNM). PENNSYLVANIA: 19.XI.1939, ex stems of *Vernonia noveboracensis* (L.) Michaux (USNM). Canada. QUEBEC: St. Romuald, 13.VI.1958, *Agromyza* (= *Hexomyza*) *schineri* on *Populus tremula tremuloides* (Michaux) Loeve & Loeve (CNCI). MANITOBA: Falcon Lake, 8.VII.1965, cynipid(?) gall on white poplar (CNCI); Riding

Mountain National Park, 7.VIII.1966, cynipid[?] gall on white poplar (CNCI). NOVA SCOTIA: Simpson Field Station (Rest. Co.), 5.VIII.1960, *Agromyza* (= *Hexomyza*) *schineri* (CNCI). ONTARIO: Ancaster, various dates in December 1966 and January 1977, *Melanagromyza martini* Spencer (CNCI), 19.XII.1966, *Phytomyza flavicornis* Fallén (Diptera: Agromyzidae) (CNCI); Vinland Station, 23.V.1936, ex *Phalonia voxana* Kft. (Lepidoptera: Cochylidae) in stems of *Prenanthes alba* L. (CNCI); Windsor, 1948, *Agromyza* sp. in hollyhock [*Melanagromyza hicksi* Steyskal ?] (CNCI). In addition, *Syntomopus americanus* has been collected in association with the following plants: alfalfa at Mesa, Arizona; *Ambrosia* at Sioux City, Iowa and Malden, Massachusetts; ragweed at St. David, Ontario; *Helianthus annuus* L. at Webster, Missouri; *Salix* at Sioux City, Iowa and Logan Canyon, Utah; *Betula* at 58 miles east of Dawson, Yukon; and *Urtica dioica* L. at Ancaster, Ontario.

There are several host records for *Syntomopus americanus* in the literature. This species was reared in the spring from stems of *Ambrosia trifida* L., probably from pupae of *Agromyza* sp. (Webster 1894). *Syntomopus americanus* emerged in January and February along with adults of its host from pupae in stems of hollyhock, *Althaea rosea* (L.) (Malvaceae), in the lab (Hansberry 1940). The host is given as *Agromyza* (= *Melanagromyza*) *angelicae* Frost; however, this agromyzid is a stem borer in *Angelica* spp. (Spencer and Steyskal 1986). The stem-mining agromyzid of hollyhock is *Melanagromyza hicksi* Steyskal and this may be the actual host in the study of Hansberry (1940). Schread et al. (1942) reported *Syntomopus americanus* as a primary parasite of dipterous larvae in stems of the dwarf ragweed, *Ambrosia artemisiifolia* L. *Syntomopus americanus* was also given as a major parasite of *Agromyza* (= *Melanagromyza*) *virens* puparia in stems of guayule, *Parthenium argentatum* Gray (Asteraceae) (Lange 1944; Cassidy et al. 1950). Parasite records of *Syntomopus americanus* in the studies by Webster, Hansberry, Lange, and Cassidy et al. were verified by me through examination of voucher material in collections.

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**Systematic studies on *Pseudomyrmex* acacia-ants
(Hymenoptera: Formicidae: Pseudomyrmecinae)**

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Abstract.—The obligate acacia-ants (*Pseudomyrmex ferrugineus* group) are well known as defensive inhabitants of swollen-thorn acacias in the northern Neotropics. A taxonomic revision of these ants leads to the recognition of ten species: *P. ferrugineus* (F. Smith), *P. flavicornis* (F. Smith), *P. janzeni*, sp. nov., *P. mixtecus*, sp. nov., *P. nigrocinctus* (Emery), *P. particeps*, sp. nov., *P. peperi* (Forel), *P. satanicus* (Wheeler), *P. spinicola* (Emery), and *P. veneficus* (Wheeler). The following new synonymy is proposed: *P. nigrocinctus* = *P. alfari* (Forel) = *P. bicinctus* (Santschi) = *P. peltatus* (Menozzi); *P. spinicola* = *P. atrox* (Forel) = *P. gaigei* (Forel) = *P. infernalis* (Wheeler) = *P. scelerosus* (Wheeler). Diagnostic descriptions and taxonomic comments are also provided for ten other unrelated species of *Pseudomyrmex* which have become secondarily associated with swollen-thorn acacias either as obligate and, in at least one case, parasitic occupants (*P. nigropilosus* (Emery), *P. simulans* Kempf and *P. subtilissimus* (Emery); *P. reconditus*, sp. nov., may also belong in this category) or as facultative inhabitants (*P. boopis* (Roger), *P. gracilis* (Fabricius), *P. hesperius*, sp. nov., *P. ita* (Forel), stat. nov., *P. kuenckeli* (Emery) and *P. opaciceps*, sp. nov.). A cladistic analysis of the *P. ferrugineus* group yields the following result which appears to be fairly robust insofar as there is congruence among the trees derived from worker-, queen-, and male-based character sets: ((*nigrocinctus* + *particeps*) + (*peperi* + ((*satanicus* + *spinicola*) + *ferrugineus* complex))). The "ferrugineus complex" comprises five species whose phylogenetic relationships are not fully clarified. The composite data set (47 characters from all three castes) supports the following partial resolution: (*ferrugineus* + *janzeni* + (*flavicornis* + (*mixtecus* + *veneficus*))). The cladogram of the *P. ferrugineus* group indicates that speciation in the group has occurred primarily as a consequence of geographical isolation, and that the ants and their host acacias have experienced diffuse coevolution rather than strict cospeciation.

INTRODUCTION

Pseudomyrmex ferrugineus (F. Smith) and related species of ants form a well-defined monophyletic group, the members of which nest exclusively in the hollow, swollen thorns of several New World *Acacia* species. Because of their aggressive behavior and predictable occurrence on the acacias, these ants have received considerable attention from tropical biologists (Belt 1874; Safford 1922; Skwarra 1934a, 1934b; Wheeler 1942; Janzen 1966, 1973). The landmark studies of Janzen (1966, 1967b) provided strong experimental evidence of the mutualistic nature of the *Pseudomyrmex/Acacia* association, and the relationship between the two organisms is often cited in discussions of coevolved mutualisms (e.g. Gilbert 1983; Beattie 1985; Futuyma 1986). At the same time, the systematics of the acacia-ants has been neglected, with the result that misidentifications and misstate-

ments have appeared in the ecological literature. In this paper I present a taxonomic revision of the obligate acacia-ants (*Pseudomyrmex ferrugineus* group) and an assessment of their phylogenetic relationships. I also attempt to clarify the identities of other, unrelated species of *Pseudomyrmex* which have become secondarily associated with swollen-thorn acacias.

The earlier taxonomic literature on acacia-ants is scattered in more than a dozen papers containing descriptions of various species, subspecies, and "varieties". Two of the more comprehensive treatments are those of Emery (1890) and Wheeler (1942). In presenting the results of his ecological studies Janzen (1966, 1967b, 1973) summarized his understanding of acacia-ant taxonomy. Ward (1989) provided a brief diagnosis of the *P. ferrugineus* group, together with taxonomic and nomenclatural notes on the commoner species.

MATERIALS AND METHODS

COLLECTIONS

Material for the present study was examined in the following collections:

- AMNH American Museum of Natural History, New York, NY, USA
- ANSP Academy of Natural Sciences, Philadelphia, PA, USA
- BMNH The Natural History Museum, London, U.K.
- CASC California Academy of Sciences, San Francisco, CA, USA
- CHAH C.H.A. Hespénheide Collection, University of California at Los Angeles, CA, USA
- CISC California Insect Survey, University of California at Berkeley, CA, USA
- CUIC Cornell University Insect Collection, Ithaca, NY, USA
- EBCC Estación de Biología Chamela, Jalisco, Mexico
- FFIC Fernando Fernández Collection, Santa Fe de Bogotá, Colombia
- GBFM Graham B. Fairchild Museo de Invertebrados, Universidad de Panamá, Panama
- GCWC G.C. & J. Wheeler Collection, Silver Springs, FL, USA
- INBC Instituto Nacional de Biodiversidad (collections previously held in MNCR: Museo Nacional de Costa Rica), San José, Costa Rica
- INHS Illinois Natural History Survey Insect Collection, Champaign, IL, USA
- JTLC J.T. Longino Collection, Evergreen State College, Olympia, WA, USA
- KSUC Kansas State University Insect Collection, Manhattan, KS, USA
- LACM Natural History Museum of Los Angeles County, Los Angeles, CA, USA
- MCSN Museo Civico di Storia Naturale, Genoa, Italy
- MCZC Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
- MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
- MNHN Muséum National d'Histoire Naturelle, Paris, France
- MZSP Museo de Zoologia da Universidade de São Paulo, Brazil
- NHMB Naturhistorisches Museum, Basel, Switzerland
- NHNV Naturhistorisches Museum, Vienna, Austria
- PSWC P.S. Ward Collection, University of California at Davis, CA, USA
- SEMC Snow Entomological Museum, University of Kansas, Lawrence, KS, USA
- UCDC Bohart Museum of Entomology, University of California at Davis, CA, USA
- UCRC UCR Entomological Collection, University of California at Riverside, CA, USA
- USNM National Museum of Natural History, Washington, DC, USA
- WPMC W.P. MacKay Collection, El Paso, TX, USA
- ZMHB Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
- ZMUC Zoologisk Museum, University of Copenhagen, Denmark
- ZMUH Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany
- ZSMC Zoologische Staatssammlung, Munich, Germany

Special mention should be made of the very large and important series of *Pseudomyrmex* collected by D.H. Janzen from 1963 to 1974 and now housed in the Natural History Museum of Los Angeles County (LACM). The Janzen material includes a large number of pinned specimens (usually glued to the side of the pin rather than point-mounted) and an extensive alcohol collection (partly overlapping with the pinned series but including additional accessions). Janzen's field notes pertaining to the collection of these ants have also been deposited in LACM. Obligate acacia-ants (*P. ferrugineus* group) constitute the bulk of the collected material. They occur as long nest series from throughout Central America, with very useful queen-male-worker associations, making this material of inestimable value to the current revision.

When the Janzen collection was received at LACM in 1984 most specimens had only code numbers associated with them—among the pinned specimens a single individual per nest series typically contained a code number, with the remaining specimens being unlabelled—and in some instances difficulties arose in retrieving full data for coded specimens from Janzen's field notes. In other cases the field notes contradicted the apparent identity or composition of a nest series. This latter problem applied mainly to pinned specimens; the alcohol material appeared to be reliably labelled or coded, i.e. the contents of the vials agreed with the field notes. Thanks to the efforts of Roy Snelling and Jack Longino, who incorporated the Janzen collection into the LACM, many of these discrepancies or uncertainties were resolved, but there remains a residue of "problem material" for which collection data are lacking or ambiguous. Among the pinned specimens this comprises twelve drawers in the LACM collection which have been specifically set aside from the main collection. None of this problematical material has been cited in the present study, but I have examined it and determined that no additional species are represented there. Although omission of this material means the potential loss of some locality data, I have examined the entire alcohol collection and point-mounted representative samples so that geographic coverage remains extensive. The main pinned series of LACM acacia-ants, i.e. that for which accurate data labels are available, comprises 30 drawers and approximately 20,000 specimens, the great majority of which were collected by Janzen.

METRIC MEASUREMENTS AND INDICES

All measurements were made under a Wild microscope at 50X power, using an orthogonal pair of Nikon micrometers wired to a digital readout. Measurement conventions follow those described in Ward (1985, 1989). Note that a full-face or dorsal view of the head involves positioning the posterior margin and the anterolateral margins (above the mandibular insertions) so that they lie in the same plane of view.

The following measurements and indices are cited in this study (the first six measurements are taken with the head in a full-face, dorsal view):

- HW Head width: maximum width of head, including the eyes.
- VW Vertex width: width of the posterior portion of the head (vertex), measured along a line drawn through the lateral ocelli.
- HL Head length: midline length of head proper, from the anterior clypeal margin to the midpoint of a line drawn across the "occipital" (i.e. posterior) margin.
- EL Eye length: length of compound eye; note that this is measured with the head in full face, dorsal view, unlike EW(below).
- OD Ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli.
- OOD Oculo-ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn across the posterior margins of the compound eyes (this distance is negative in value if the posterior margin of the compound eye exceeds the median ocellus).
- MFC Minimum frontal carinal distance: minimum distance between the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites.
- ASD Antennal sclerite distance: maximum distance between the lateral margins of the median lobes of the antennal sclerites, measured in full-face, dorsal view of the head.
- ASO Antennal sclerite distance, outer margins: maximum distance between the outer, lateral margins of the antennal sclerites.
- CLW Width of median clypeal lobe, measured between the anterolateral angles (in *Pseudomyrmex satanicus* and *P. spinicola* only; see Figs. 10, 11).
- MD4, MD5, MD8, MD9 A series of mandibular measurements (see Ward 1989, figure 2). MD4: distance along the basal margin of the mandible from the base to the mesial basal tooth; MD5: length of the basal margin; MD8: distance along the masticatory margin from the apex to the fourth tooth, counting from the apex; MD9: length of the masticatory margin.

- EW Eye width: maximum width of compound eye, measured along its short axis in an oblique dorsolateral view of the head.
- SL Scape length: length of the first antennal segment, excluding the radicle.
- LF1 Length of first funicular segment: maximum measurable length of the first funicular segment (pedicel), including its basal articulation in workers and queens but excluding the basal articulation in males (where it is usually hidden).
- LF2 Length of second funicular segment: maximum measurable length of the second funicular segment.
- LF3 Length of third funicular segment: maximum measurable length of the third funicular segment.
- WF2 Width of second funicular segment.
- FL Profemur length: length of the profemur, measured along its long axis in posterior view (see Ward 1985, figure 3).
- FW Profemur width: maximum measurable width of the profemur, measured from the same view as FL, at right angles to the line of measurement of FL.
- DPL Diagonal length of the propodeum: length of the propodeum, measured in lateral view along a diagonal line drawn from the "metapleural" lobe to the metanotal groove (see Ward 1985, figure 2).
- BF Length of the basal (=dorsal) face of the propodeum, measured in lateral view from the metanotal groove to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.
- DF Length of the declivitous face of the propodeum, measured in lateral view from the "metapleural" lobe to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.
- MP Depth of metanotal groove ("mesopropodeal impression"), measured in lateral view from the bottom of the metanotal groove to a line drawn across the dorsal surface of the mesonotum and propodeum.
- PL Petiole length: length of the petiole, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (see Ward 1985, figure 4).
- PND Petiolar node distance: distance from the lateral flanges of the anterior petiolar peduncle to the maximum height of the node, measured from the same view as PL and along the same line of measurement (see Ward 1985, figure 4).
- PH Petiole height: maximum height of the petiole, measured in lateral view at right angles to PL, but excluding the anteroventral process.
- PPL Postpetiole length: length of the postpetiole, measured in lateral view, from the anterior peduncle (of the postpetiole) to the point of contact with the fourth abdominal tergum, excluding the pretergite (see Ward 1985, figure 4).
- DPW Dorsal petiolar width: maximum width of the petiole, measured in dorsal view.
- MPW Minimum petiolar width: minimum width of the petiole, measured in dorsal view, anterior to DPW.
- PPW Dorsal postpetiolar width: maximum width of the postpetiole, measure in dorsal view.
- LHT Length of metatibia: maximum measurable length of metatibia, excluding the proximal part of the articulation which is received into the distal end of the metafemur (see Ward 1989, figure 5).
- CI Cephalic index: HW/HL
- OI Ocular index: EW/EL
- REL Relative eye length: EL/HL
- REL2 Relative eye length, using HW: EL/HW
- OOI Oculo-ocellar index: OOD/OD
- VI Vertex width index: VW/HW
- FCI Frontal carinal index: MFC/HW
- FCI2 Frontal carinal index, using ASD: MFC/ASD
- ASI Antennal sclerite index: ASD/ASO
- SI Scape index: SL/HW
- SI2 Scape index, using EL: SL/EL
- FLI Funicular length index: (LF2 + LF3)/WF2
- FI Profemur index: FW/FL
- PDI Propodeal index: BF/DF
- MPI Metanotal index: MP/HW
- NI Petiole node index: PND/PL

- PL1 Petiole length index: PH/PL
 PL12 Petiole length index, using PPL: PPL/PL
 PW1 Petiole width index: DPW/PL
 PW12 Petiole width index, using PPW: DPW/PPW
 PW13 Petiole width index, using MPW: MPW/DPW
 PW14 Petiole width index, using LHT: DPW/LHT
 PPW1 Postpetiole width index: PPW/PPL

Other Conventions

Other terminology follows the usage in Ward (1989). Note that descriptions of surface sculpture and integument reflectance apply to observations made under soft light, with an opaque (Mylar) filter placed between the specimens and source of illumination. Palp formula refers to the number of maxillary palp segments followed by the number of labial palp segments; 5p4.3 indicates a condition intermediate between 5.3 and 4.3, i.e. partial fusion of the fourth and fifth maxillary palp segments.

Listing of synonymy under each species is restricted to citation of the original descriptions (with full reference given for all previously proposed junior synonyms) and new nomenclatural combinations. For ecologists a more useful summary of name usage is offered in Table 1, which indicates the correspondences between the names appearing in the biological literature on acacia-ants and the currently valid scientific names. The reader will appreciate that there has been considerable misidentification of these ants.

In the lists of material examined of each species, I have cited only locality and collector ("c.u." signifies collector unknown), with the source collections listed together at the beginning. Additional locality information is sometimes provided in square brackets, to facilitate location of the collecting site. Considerable effort was expended to determine the coordinates (latitude and longitude) of each collecting site, and this was then used in conjunction with the public domain software program Versamap (version 1.20) to plot the distributions of each species (Figs. 67-72).

Cladistic Analysis

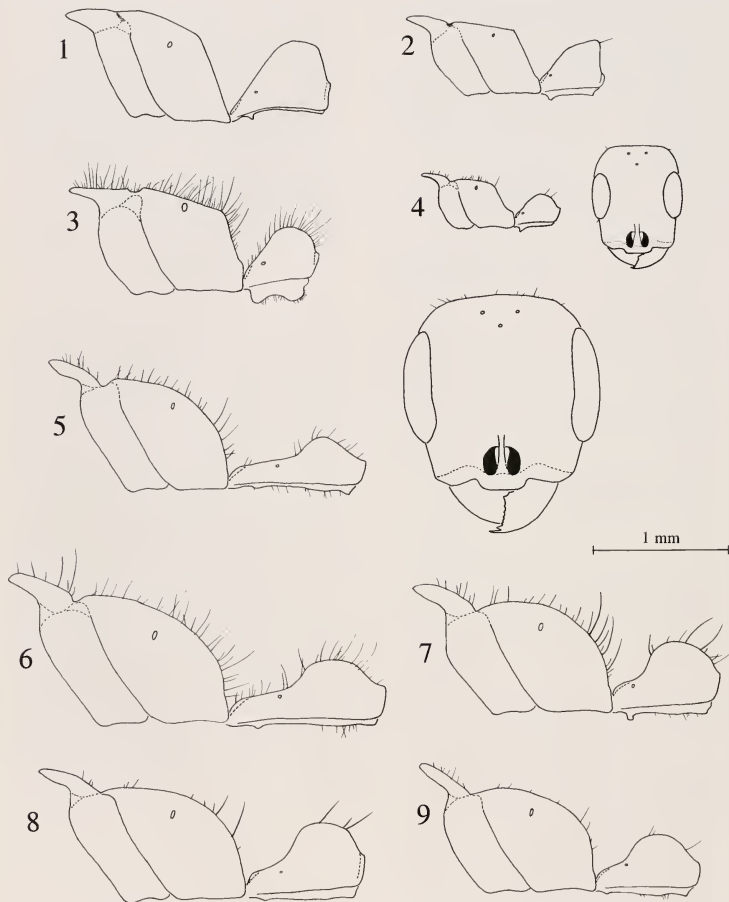
A set of 47 characters, representing the most discrete or quantifiable differences among species or groups of species in the *P. ferrugineus* group, was used for phylogenetic analysis. Twenty of these characters were worker-based (11 of these manifested the same conditions in queens), 8 were queen-based, and 19 were taken from male morphology, primarily male genitalia. The characters and character states are as follows:

1. Worker, median clypeal lobe (0) laterally rounded or subangulate, (1) laterally with sharp angles or teeth (Figs. 10, 11).
2. Worker and queen, frontal carinae (0) relatively well separated, median lobes of antennal sclerites less exposed (Figs. 12-19, 32), (1) closely adjacent and median lobes of antennal sclerites more exposed (Figs. 10, 11, 32).
3. Worker and queen, palp formula (0) 5.3, (1) 4.3.
4. Worker, head (0) broader, relative to HL, DPL and PL, (1) narrower; see regressions of HL, DPL and PL on HW (Figs. 36-38).
5. Worker, scape (0) short, relative to HL, (1) longer; regression of SL on HL lying above that of other species.
6. Worker, conspicuous pit-like impression on midline of head (0) absent, (1) present.
7. Worker, petiole (0) short relative to postpetiole, PL12 0.77, (1) longer relative to postpetiole, PL12 < 0.77.
8. Worker and queen, petiole (0) without a well differentiated anterior peduncle, i.e. weakly constricted in dorsal view and with little or no inflection of the anterior face of the petiole in lateral profile (Figs. 22, 23), (1) with a well differentiated peduncle (Figs. 20, 21, 24-29).
9. Worker and queen, petiole, dorsal view, angulate posterolateral corners (0) absent, (1) moderately developed, preceded by convex or sinuate sides (e.g. Figs. 20, 27), (2) very prominent, preceded by more or less straight sides (Fig. 24).
10. Worker and queen, petiole (0) shorter and higher, worker PL1 0.71, queen PL1 0.64,

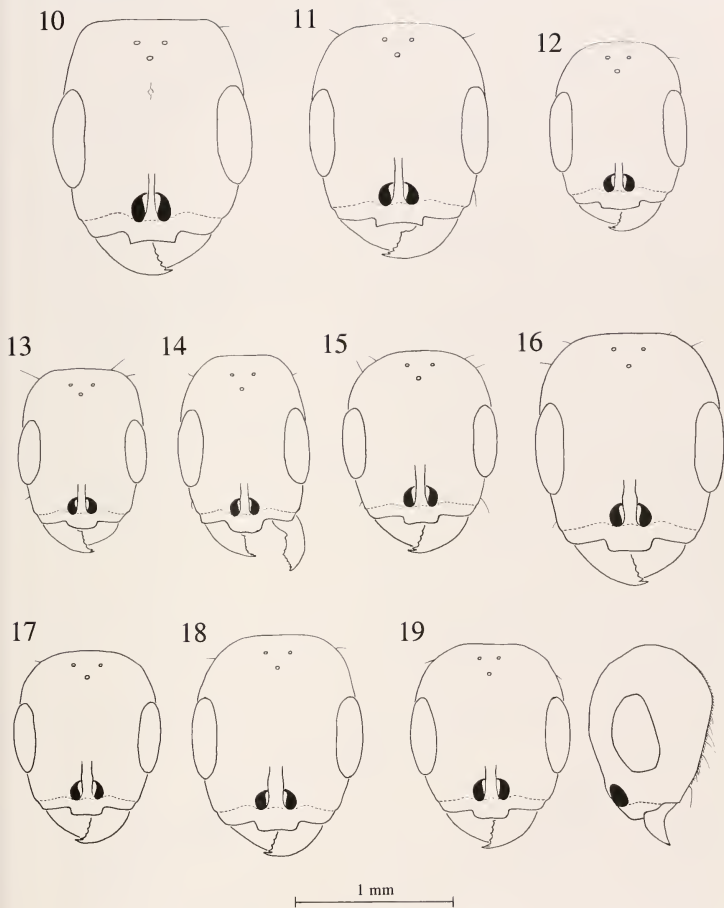
- (1) more slender, worker $PLI < 0.72$, queen $PLI < 0.64$.
11. Worker, DPW relative to HW (0) narrow, (1) broader, (2) very broad; see regression of DPW on HW (Fig. 41).
 12. Worker, plot of PW13 by HW lying in (0) upper left (1) lower right (2) lower left region, of Fig. 39.
 13. Worker and queen, plot of PW14 by HW lying in (0) center and lower right (1) upper left (3) lower left region, of Fig. 40.
 14. Worker, postpetiole (0) broad, PPWI > 1.30 , (1) narrow, PPWI 1.00-1.30.
 15. Worker, metatibia (0) short, relative to HL, (1) relatively long; see regression of LHT on HL (Fig. 30).
 16. Worker and queen, head sculpture (0) densely punctulate, subopaque to sublucid, at least on upper third of head, (1) densely punctulate, opaque, (3) punctulate-coriarious, opaque (matte).
 17. Worker and queen, propodeum, posterolateral portions (0) sublucid, without overlying rugulo-punctate sculpture, (1) supopaque to opaque, with rugulo-punctate sculpture.
 18. Worker and queen, petiolar node (0) lacking conspicuous suberect pubescence, (1) with such pubescence.
 19. Worker and queen, standing pilosity on external faces of tibiae (0) present, (1) absent.
 20. Worker and queen, head and gaster (0) yellow- to orange-brown, (1) reddish-brown to medium or dark brown, (2) very dark brown to black (excluding mandibles, clypeus and scape).
 21. Queen, size (0) small, HW 0.85, (1) medium to large, HW 0.85.
 22. Queen, head shape, for a given LHT (0) elongate, (1) less elongate, (2) broad (see Fig. 52).
 23. Queen, petiole (0) short, relative to HW, $PL/HW < 0.71$, (1) longer, $PL/HW > 0.71$.
 24. Queen, petiole (0) short, relative to HL, (1) longer: see regression of PL on HL (Fig. 46).
 25. Queen, regression of PH on HW lying in (0) upper (1) middle (2) lower region, in Fig. 47.
 26. Queen, petiole, dorsal view (0) narrow, relative to HL, (2) broader; regression of DPW on HL lying above that of other species.
 27. Queen, metatibia (0) short, relative to HL, $LHT/HL < 0.62$, (1) longer, $LHT/HL > 0.66$.
 28. Queen, metatibia (0) short, relative to HW, (1) longer; see regression of LHT on HW (Fig. 31).
 29. Male, head (0) narrower, CI 0.82-0.94 and $HW < 0.96$, (1) broader, CI 0.94 and/or $HW > 0.96$ (regression of HL on HW lying below that of other species).
 30. Male, scape index (SI) (0) 0.22-0.30, (1) 0.29-0.35, and regression of SL on HW lying above that of other species.
 31. Male, scape length, relative to EL and HL (0) long, $SI2 \ 0.43-0.56$, $SL/HL \ 0.22$, (1) shorter, $SI2 \ 0.33-0.43$, $SL/HL \ 0.21$ (and regression of SL on HL lying below that of other species).
 32. Male, compound eye length, relative to HW (0) long, $REL2 \ 0.56-0.63$, (1) shorter, $REL2 \ 0.49-0.58$, and regression of EL on HW lying below that of other species.
 33. Male, petiole (0) less slender, $PLI > 0.45$, (1) more slender, $PLI < 0.50$, and regressions of PH and DPW on LHT lying below those of other species.
 34. Male, sternite IX, posterior margin (0) convex, (1) with a moderate concavity, less than semicircular (Fig. 54), (2) with a deep, semicircular concavity (Fig. 55).
 35. Male, paramere, lateral view, posterodorsal extremity (0) rounded, (1) angulate or expanded.
 36. Male, paramere, lateral view, posterodorsal extremity (0) not projecting caudad, (1) projecting caudad, as in Figs. 56, 57.
 37. Male, paramere, lateral view, posterodorsal extremity (0) not developed as a lobe-like protrusion, whose mesial face is a saucer-like concavity, (1) so developed (Figs. 61-66).
 38. Male, paramere, lateral view, posterodorsal extremity (0) well separated from mesiodorsal lobe, (1) close to mesiodorsal lobe, enclosing a narrow space between it and the lobe (Figs. 58, 61-66).
 39. Male, paramere, digitiform mesiodorsal lobe (0) absent, (1) present, slender, directed poste-

- riorly or posterodorsally (Figs. 56-60, 63-65), (2) present, stubby, directed more or less dorsally (Figs. 61, 62).
40. Male, paramere, mesial face of posterodorsal extremity (0) simple in form, not expanded mesially, (1) expanded mesially, partly obscuring the mesial dorsoventral ridge in posterior view.
 41. Male, aedeagus, posterior margin (0) entire, not medially pointed, (1) toothed, and medially pointed.
 42. Male, aedeagus, posterior margin (0) bent posterolaterally, (1) bent anterolaterally, (2) bent anterolaterally but with the medial point redirected posteriorly.
 43. Male, aedeagus, laterally bent portion of posterior margin (0) continuous with the margin of the posterodorsal extremity, (1) discontinuous with margin of posterodorsal extremity (elevated laterally), the two connected by a gradual slope, (2) discontinuous with margin of posterodorsal extremity, elevated laterally, and separated by a trenchant rise (posterior view) from the posterodorsal extremity.
 44. Male, aedeagus, plate-like expansion of posterodorsal extremity (0) absent, (1) moderately developed, (2) strongly developed.
 45. Male, aedeagus, external face (0) without a large, central elevated area, (1) with a central elevated area, delimited posteroventrally by a weak ridge or carina, (2) with a central elevated area, delimited posteroventrally by a strong lamellate carina.
 46. Male, aedeagus, external face, aforementioned carina (if present) (0) well separated from the toothed posterior margin, (1) running close to and more or less parallel with the toothed posterior margin but separated by a deep groove, (2) converging posterodorsally with the toothed posterior margin.
 47. Male, aedeagus, posteroventral extremity (0) broadly rounded, (1) subangulate, (2) angulate with a tooth-like protrusion.

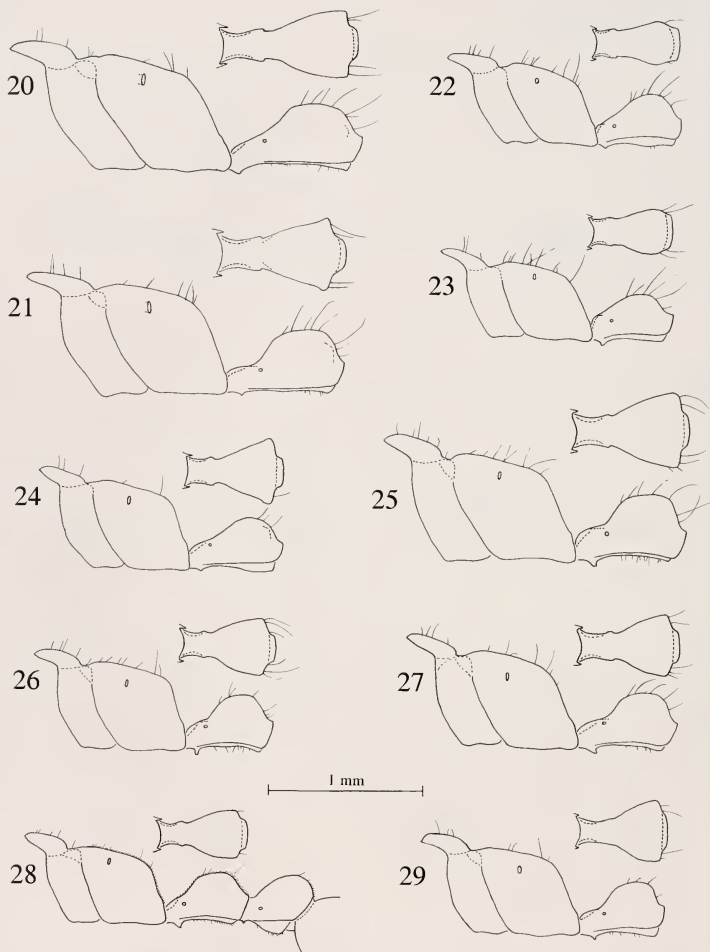
The data set was analyzed using Farris' Hennig86 program. Characters 12, 13 and 16 were considered unordered. As an outgroup I chose *Pseudomyrmex fervidus* (F. Smith), a Central American species which shares a number of (mostly worker) features in common with the *P. ferrugineus* group: 5,3 palp formula, similar mandibular dentition, well developed metanotal groove, abundant pilosity on mesosoma dorsum, relatively small eyes, and a similar habitus with respect to size and color. In a few instances the outgroup species spanned the phenotypic gap between two discrete states in the ingroup; it was then coded as unknown for that character. In addition to seeking the most parsimonious tree for the entire data set (rooted with the outgroup), I also compared the cladograms based on three subsets, derived from the worker, queen, and male characters sets, respectively. For this second analysis the queen character set included the eight characters assessed only in queens (21-28) plus those manifested identically in workers and queens (2, 3, 8-10, 13, 16-20), for a total of 19 characters.



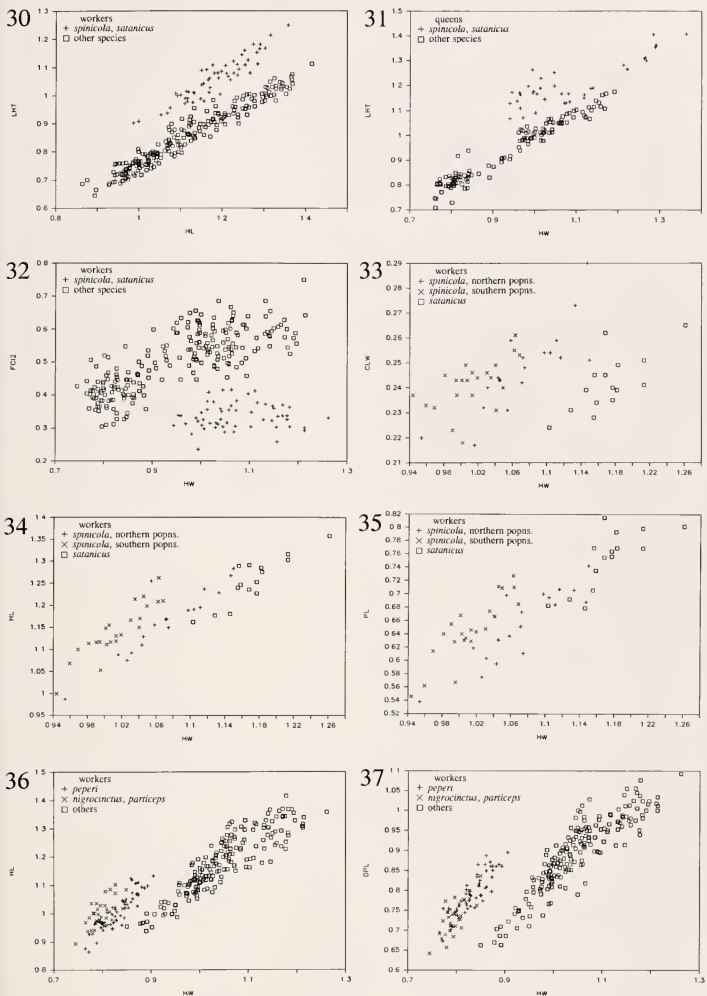
Figs. 1-9. *Pseudomyrmex* workers, lateral view of mesonotum, propodeum and petiole, with pilosity shown in outline; Figs. 4 and 5 include a frontal view of worker head. 1, *P. boopis* (Costa Rica); 2, *P. ita* (Costa Rica); 3, *P. kuenckeli* (Costa Rica); 4, *P. hesperius* (Mexico, paratype); 5, *P. opaciceps* (Guatemala, paratype); 6, *P. gracilis* (Mexico); 7, *P. nigropilosus* (Costa Rica); 8, *P. reconditus* (Nicaragua, holotype); 9, *P. simulans* (Panama).



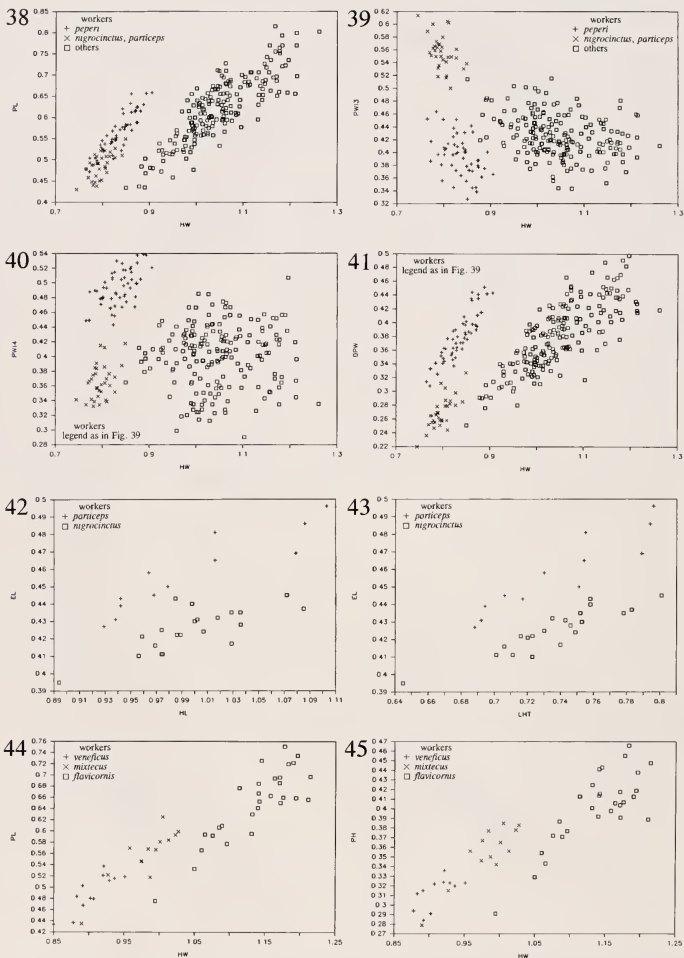
Figs. 10-19. *Pseudomyrmex ferrugineus* group, workers, full-face dorsal (=frontal) view of head with pilosity shown in outline (except on mandibles); Fig. 19 includes a lateral view of head. 10, *P. satanicus* (Panama); 11, *P. spinicola* (Costa Rica); 12, *P. peperi* (Guatemala); 13, *P. nigrocinctus* (Costa Rica); 14, *P. particeps* (Costa Rica, holotype); 15, *P. mixtecus* (Mexico, holotype); 16, *P. flavicornis* (Nicaragua); 17, *P. veneficus* (Mexico); 18, *P. ferrugineus* (Mexico); 19, *P. janzeni* (Mexico, holotype).



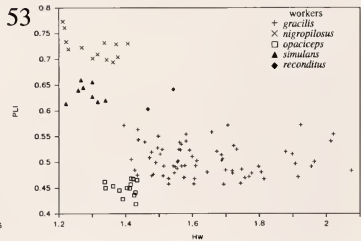
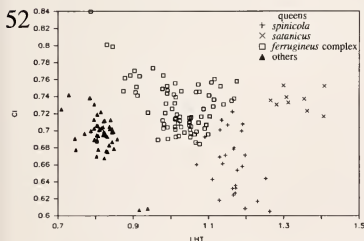
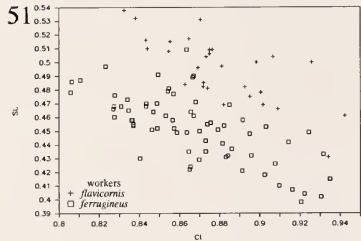
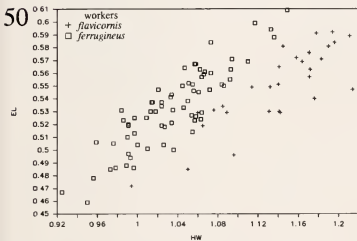
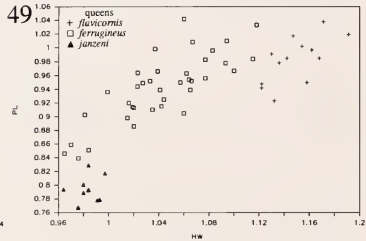
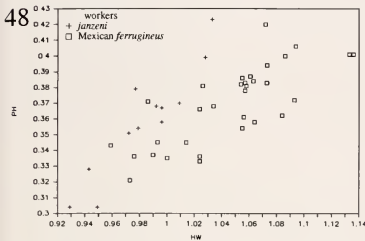
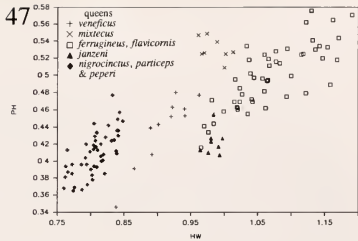
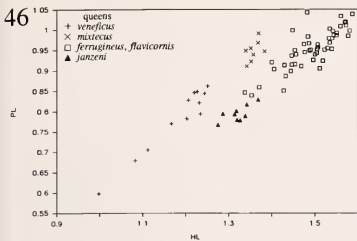
Figs. 20-29. *Pseudomyrmex ferrugineus* group, workers, dorsal view of petiole paired with lateral view of mesonotum, propodeum, petiole and, in Fig. 28, postpetiole. Standing pilosity shown in outline. 20, *P. satanicus*; 21, *P. spinicola*; 22, *P. nigrocinctus*; 23, *P. particeps*; 24, *P. peperi*; 25, *P. flavicornis*; 26, *P. mixtecus*; 27, *P. ferrugineus*; 28, *P. veneficus*; 29, *P. janzeni*. These are the same individuals illustrated in Figs. 10-19.



Figs. 30-37. Scattergram plots of various metric measurements and indices in workers and queens of the *Pseudomyrmex ferrugineus* group. "other species" refers to all others in the *P. ferrugineus* group.



Figs. 38-45. Scattergram plots of various metric measurements and indices in workers of the *Pseudomyrmex ferrugineus* group. "others" refers to all other species in the *P. ferrugineus* group.



Figs. 46-53. Scattergram plots of various metric measurements and indices in *Pseudomyrmex* workers and queens. 46-52, *P. ferrugineus* group; "others" refers to all other species in the *P. ferrugineus* group; "*P. ferrugineus* complex" refers to a complex of five species: *ferrugineus*, *flavicornis*, *janzeni*, *mixtecus* and *veneficus*; 53, *P. gracilis* group.

KEY TO *PSEUDOMYRMEX* SPECIES ASSOCIATED WITH SWOLLEN-THORN ACACIAS
(BASED ON WORKERS AND QUEENS)

The following key includes all species of *Pseudomyrmex* which have been found inhabiting swollen-thorn acacias in Mexico, Central America, or Colombia. *Pseudomyrmex* ants can be distinguished from others by their possession of a distinct postpetiole (i.e. "waist" consists of two nodes), well developed stinging, relatively large eyes (eye length more than one-third head length), and short antennal scapes (one half head width or less). In the key below, species of *Pseudomyrmex* which are believed to be obligate inhabitants of acacia are in **bold print**. These species are typically rather aggressive (but this is not true of *P. subtilissimus* or *P. nigropilosus*), while the remaining facultative inhabitants are timid, generalist, stem-nesting *Pseudomyrmex* which usually occupy swollen-thorn acacias only sporadically. Couplets 11-19 cover the *P. ferrugineus* group, the principal group of obligate acacia-ants and the focus of this study. Taxonomic comments on the other *acacia*-inhabiting species are presented in a later section of the paper (pp. 153- 162). Worker sizes exclude nanitic workers, i.e. the first-emerging miniature workers associated with colony-founding queens.

1. Standing pilosity very sparse on the head, including the gula (underside), and on the mesosoma; 1.0, and 0-1 pairs of erect setae on the pronotum, mesonotum, and propodeum, respectively, of the worker 2
- Standing pilosity common to abundant on most parts of the body, including the gula and mesosoma; worker usually with more than 10 standing hairs visible in outline on the mesosoma dorsum, not arranged in isolated pairs 4
2. Very small, light brown species (worker and queen HW < 0.60), with elongate head (CI < 0.66) and low, dorsally flattened petiole (PLI < 0.76) (Nicaragua, Costa Rica) ***subtilissimus* (Emery)**
- Larger species (worker and queen HW > 0.70), with broader head (CI > 0.70) and higher petiole (PLI > 0.80) (Figs. 1,2) 3
3. Smaller species (worker and queen HW < 1.00), with posterodorsally angulate petiole (Fig. 2) (Mexico to Colombia) ***ita* (Forel)**
- Larger species (worker and queen HW > 1.15), with posterodorsally rounded petiole (Fig. 1) (Mexico to Ecuador, Brazil) ***boopis* (Roger)**
4. Head with scattered, fine punctulae on a smooth, shiny background; punctulae on upper third of head separated by several times their diameters or more 5
- Head opaque to sublucid, more coarsely and densely punctulate, the punctulae subcontiguous on most parts of the head 6
5. Larger species (HW > 1.20), with broad head (CI 1.12) and abundant long pilosity (Fig. 3) (Mexico to Argentina, Brazil) ***kuenckeli* (Emery)**
- Small species (HW < 0.72), with elongate head (CI 0.80) and shorter, sparser pilosity (Fig. 4) (Mexico) ***hesperius*, sp.nov.**
6. Eyes relatively large and elongate (e.g. Fig. 5), eye length more than one-half head length (worker and queen REL 0.52-0.65); pronotum laterally submarginate; outer surfaces of tibiae usually with standing pilosity (may be very short); larger species, worker HW > 1.20; palp formula 6,4 7
- Eyes smaller (Figs. 10-19), usually less than one-half head length (worker and queen REL 0.38-0.50); pronotum laterally rounded; outer surfaces of tibiae without standing pilosity; medium-sized species, worker HW < 1.28; palp formula 5,3or 4,3 (***ferrugineus* group**) 11
7. Petiole long and slender, with a well developed anterior peduncle (worker and queen PLI 0.42-0.57)

(Figs. 5,6) 8

— Petiole less elongate, with a short anterior peduncle (PLI > 0.59) (Figs. 7-9, 53) 9

8. Head densely punctulate-coriarius, presenting a matte appearance; head and mesosoma black, with a contrastingly pale orange petiole, postpetiole, and gaster; petiole very slender, worker PLI 0.42-0.47 (Figs. 5, 53) (southern Mexico, Guatemala) *opaciceps*, sp. nov.

— Head densely punctulate but retaining a subopaque to sublucid (not matte) appearance; color variable but without the preceding pattern in Mexico or Guatemala; petiole usually less slender, worker PLI 0.46-0.57 (Figs. 6, 53) (throughout the Neotropics) *gracilis* (Fabricius)

9. Larger species (worker HW 1.47-1.54, queen HW 1.66), with broad head (worker CI 1.00-1.02, queen CI 0.92) (Nicaragua) *reconditus*, sp. nov.

— Smaller species (worker HW 1.21-1.41, queen HW 1.15-1.36); head more elongate (worker CI 0.84-0.90, queen CI 0.77-0.80) 10

10. Standing pilosity short, pale and inconspicuous (Fig. 9); pronotum sharply margined laterally; petiole longer, worker PLI 0.61-0.66, queen PLI 0.63-0.68; color black (Panama) *simulans* **Kempf**

— Standing pilosity long and conspicuous, with long curved black setae arising from the propodeum and petiole (Fig. 7); pronotum with blunter lateral margination; petiole short and high, worker PLI 0.69-0.77, queen PLI 0.68-0.75; color variable, usually pale or bicolored (Mexico to Costa Rica) *nigropilosus* (Emery)

11. Median clypeal lobe of worker concave, with sharp lateral angles or teeth (Figs. 10, 11); legs long in relation to body size (Figs. 30, 31); larger species (worker HW > 0.92, worker LHT > 0.88, queen HL > 1.40, queen LHT > 1.05); frontal carinae closely contiguous, worker FC12 0.24-0.42 (Fig. 32); propodeum punctulate to coriarius-imbricate, posterolateral portions sublucid with little or no overlying, coarse, rugulo-punctate sculpture 12

— Median clypeal lobe of worker laterally rounded or subangulate (without sharp angles or teeth) (Figs. 12-19); legs shorter in relation to body size (Figs. 30, 31); size variable but if as large as the preceding (worker HW > 0.92, etc.) then frontal carinae relatively well separated, worker FC12 > 0.43 (Fig. 32), and posterolateral portions of propodeum opaque to subopaque, overlain by coarse (although often weak and ill-defined) rugulo-punctate sculpture 13

12. Larger species (worker HW > 1.09, queen HW > 1.20); head broader, its posterior margin straight and rounding rather sharply into the sides (Figs. 10, 34); median clypeal lobe of worker longer and narrower (Fig. 33); worker with a conspicuous, pit-like impression on midline of head, anterior to the median ocellus; palp formula 4,3 (Panama) *satanicus* (**Wheeler**)

— Smaller species (worker HW 0.94-1.15, queen HW 0.94 - 1.14), with head a little less broad and its posterior margin rounding more gently into the sides (Figs. 10, 34); median clypeal lobe of worker notably shorter and broader (Fig. 33); worker usually lacking a pit-like impression on mid-line of head; palp formula almost invariably 5,3, rarely 5p4,3 (Honduras to Colombia) *spinicola* (Emery)

13. Smaller species (worker HW 0.74-0.90, queen HW 0.76-0.85); head, propodeum, and petiole more elongate, for a given head width (Figs. 36-38) 14

— Larger species (worker HW 0.85-1.21, queen HW 0.84-1.19); head, propodeum, and petiole shorter, for a given head width (Figs. 36-38) 16

14. Petiole and postpetiole very broad (worker PWI 0.63-0.75, worker PWI3 0.33-0.46, worker PPWI 1.41-1.83; queen PWI2 0.69-0.78) (Figs. 40, 41), the petiolar node with conspicuous posterolateral angles, in dorsal view (Fig. 24); head very finely and densely punctulate-coriarius, presenting a matte (opaque) appearance; palp formula 4,3 (Mexico to Nicaragua) *peperi* (**Forel**)

— Petiole and postpetiole relatively narrow (worker PWI 0.49-0.61, worker PWI3 0.50-0.61, worker PPWI 1.03-1.30; queen PWI2 0.57-0.63), the petiolar node without conspicuous posterolateral angles

- (Figs. 22,23); head densely punctulate, sublucid to subopaque, but without a matte appearance; palp formula 5,3 15
15. Workers and queens light orange-brown, with a fuscous patch on anterior third of abdominal tergite IV (first gastric tergite); eyes relatively short (worker EL/LHT 0.56-0.61, queen REL2 0.58-0.66) (Figs. 13, 42, 43); queen head less elongate (queen CI 0.67-0.72) (Guatemala to Costa Rica) *nigrocinctus* (Emery)
- Workers and queens entirely dark brown; eyes longer (worker EL/LHT 0.59-0.64, queen REL2 0.69-0.70) (Figs. 14, 42, 43); queen head more elongate (CI 0.61, in the two known specimens) (Costa Rica) *particeps*, *sp. nov.*
16. Small species (worker HW 0.85-0.95, queen HW 0.84-0.96) with head, gaster, and at least part of mesosoma very dark brown to black; body pubescence dense, decumbent to suberect, and conspicuous, especially on the petiolar node (Fig. 28); standing pilosity often (not always) sparse; head weakly shining (western Mexico) *veneficus* (Wheeler)
- Body pubescence dense but predominantly appressed, petiolar node without conspicuous suberect pubescence; usually larger (worker HW 0.89-1.21, queen HW 0.96-1.19) with more conspicuous standing pilosity; color and head sculpture variable 17
17. Head and gaster (typically also mesosoma) very dark brown to black; head densely punctulate and opaque 18
- Body lighter in color: light orange-brown to medium brown, rarely dark brown; head at least weakly sublucid between ocelli and upper margin of the compound eye 19
18. Smaller species, worker HW 0.89-1.03, queen HW 0.96-1.01; petiole relatively longer and higher (Figs. 44-47) (southern Mexico) *mixtecus*, *sp. nov.*
- Larger species, worker HW 0.99-1.21, queen HW > 1.10; petiole relatively shorter and lower (Figs. 44-47) (Guatemala to Costa Rica) *flavicornis* (F. Smith)
19. Head and mesosoma light orange-brown, the gaster similar or slightly darker; underside of head (gula) with conspicuous suberect pubescence (Fig. 19); profile of worker mesosoma as in Fig. 29; smaller species (worker HW 0.93-1.03, queen HW 0.96-1.00) with shorter, higher petiole (Figs. 46-49) (western Mexico) *janzeni*, *sp. nov.*
- Gaster (and usually head) medium to dark brown, mesosoma variable; gular pubescence usually more appressed and inconspicuous; in profile worker mesosoma usually with basal face rounding more gradually into declivitous face (Fig. 27); size variable but larger on average (worker HW 0.92-1.15, queen HW 0.92-1.12), with longer and lower petiole (Figs. 46-49) (eastern and southern Mexico to Honduras) *ferrugineus* (F. Smith)

KEY TO MALES OF THE OBLIGATE ACACIA-ANTS,
PSEUDOMYRMEX FERRUGINEUS GROUP

Although isolated acacia-ant males are unlikely to be encountered, the following key is offered as a supplement for determination of species in the *P. ferrugineus* group. It can be used to confirm worker- or queen-based identifications, but some couplets require examination of the male genitalia.

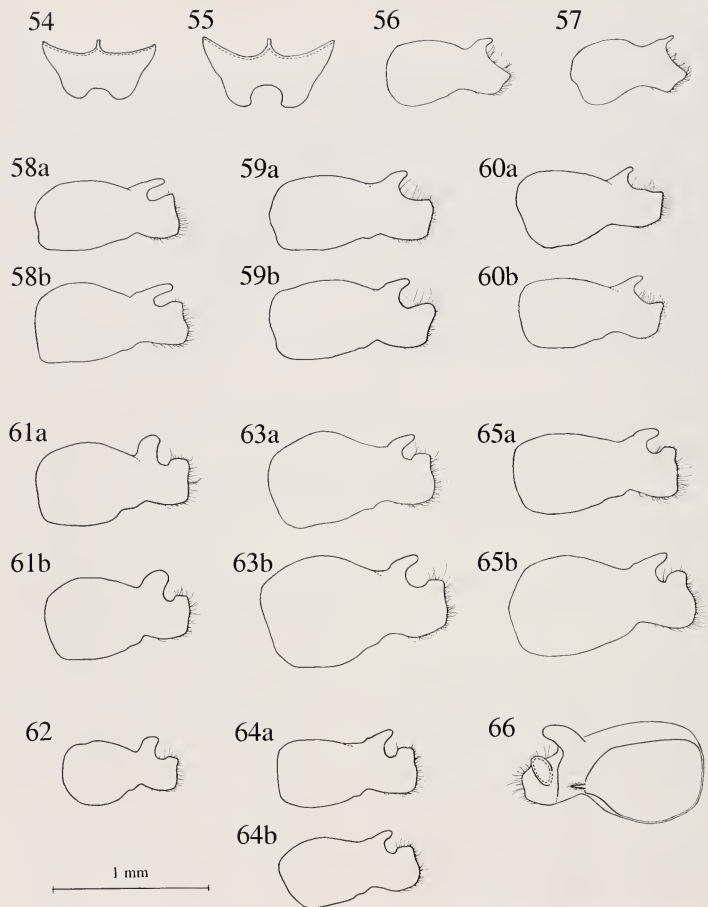
1. Posterior margin of subgenital plate (sternite IX) with a shallow (less than semicircular) concavity (Fig. 54); scape short, SI2 0.33-0.43, SL/HL 0.21 2
- Posterior margin of subgenital plate (sternite IX) with a deep, semicircular concavity (Fig. 55); scape longer, SI2 0.43-0.56, SL/HL 0.22 3
2. Paramere, in lateral view, with a slender finger-like mediodorsal lobe and angulate posteroventral corner (Fig. 57) *particeps*
- Paramere, in lateral view, with a stubbier mediodorsal lobe and more gently rounded posteroventral

corner (Fig. 56)	<i>nigrocinctus</i>
3. Scape and compound eye longer, relative to HW (SI 0.29-0.35; REL2 0.56-0.62 (n=6)); head narrower, CI 0.82-0.94, HW 0.81-0.95; lateral view of paramere as in Figs. 58a, 58b	<i>peperi</i>
— Scape and compound eye shorter (SI 0.22-0.30, REL2 0.49-0.58); head broader, CI 0.94 and/or HW 0.96; lateral view of paramere not as in Figs. 58a, 58b	4
4. Paramere, in lateral view, with posterodorsal corner well separated from mediodorsal lobe (Figs. 59-60)	5
— Paramere, in lateral view, with posterodorsal corner bent upward and enclosing a space between itself and the mediodorsal lobe which is subequal to the area of the latter (Figs. 61-65)	6
5. Lateral view of paramere as in Figs. 59a and 59b: mediodorsal lobe relatively broad and partly enclosing a space between itself and the posterodorsal corner; larger species, HW 1.06-1.09 (n=5)	<i>satanicus</i>
— Paramere typically as in Fig. 60a, with mediodorsal lobe more slender and more distant from posterodorsal corner (Fig. 60b depicts a less typical male, from Colombia); smaller species, HW 0.92-1.05 (n=12)	<i>spinicola</i>
6. Mediodorsal lobe of paramere stout, directed more or less dorsally (Figs. 61, 62)	7
— Mediodorsal lobe of paramere more slender and directed posterodorsally (Figs. 63-65)	8
7. Body pubescence dense and conspicuous, suberect on dorsum of head, propodeum and petiole; smaller species, HW 0.79-0.88 (n=7)	<i>veneficus</i>
— Body pubescence less dense and less conspicuous, predominantly appressed or decumbent on the propodeum and petiole; larger species, HW 0.88-0.97 (n=6)	<i>mixtecus</i>
8. Smaller species, HW 0.93-0.96 (n=6)	<i>janzeni</i>
— Larger species, HW 0.99-1.19 (n=22)	<i>ferrugineus</i> and <i>flavicornis</i>

PSEUDOMYRMEX FERRUGINEUS GROUP
Introduction

Worker, diagnosis.—Medium sized species (HW 0.74-1.26, HL 0.86-1.42); head varying from moderately elongate to rather broad (CI 0.75-0.97), with relatively short eyes (REL 0.39-0.50, REL2 0.45-0.62) (Figs. 10-19). Masticatory margin of mandible with 6, rarely 7, teeth, MD8/MD9 0.70; mesial tooth on basal margin notably closer to apicobasal angle than to proximal tooth, MD4/MD5 0.74. Palp formula 5,3, reduced to 4,3 in two species. Anterior margin of median clypeal lobe somewhat blunt-edged, in dorsal view convex, straight or concave, laterally rounded or with sharp angles. Frontal carinae separated by about basal scape width in most species but more closely contiguous in two (FC10.03-0.10, FC12 0.24-0.75, AS1 0.52-0.73), fusing anterolaterally with antennal sclerites. Funicular segments II and III about as broad as long (FLI 1.46-2.45). Profemur slender (FI 0.35-0.41). Pronotum laterally rounded. Metanotal groove well marked (MPI 0.04-0.09). Basal and declivitous faces of propodeum moderately well

differentiated and subequal in length (PDI 0.94-1.30), in profile the juncture between the two subangulate or gently rounded (Figs. 20-29). Petiole relatively long (PL/HL 0.44-0.63), always much longer than high or wide (PLI 0.47-0.71, PW1 0.46-0.75), small anteroventral tooth present; in two species anterior peduncle of petiole weakly differentiated and posterolateral corners of petiolar node not expanded (these are presumably the plesiomorphic conditions in the group), in other species petiole with distinct anterior peduncle and with expanded, (sub)angulate posterolateral corners. Postpetiole broader than long (PPWI 1.03-1.85), with small anteroventral tooth. Body sculpture varying from densely punctulate or punctulate-coriarius to coriarius-imbricate, the integument sublucid to opaque; dorsum of head never with extensive smooth, shiny interspaces (punctulae usually separated by their diameters or less); propodeum of some species overlain by a coarser but weak rugulo-punctate sculpture. Standing pilosity common, present on the scapes, head, entire mesosoma dorsum (10 or more standing hairs visible in profile), petiole, postpetiole and gaster,



Figs. 54-66. *Pseudomyrmex ferrugineus* group, male terminalia. Figs. 54-55: sternite IX; Figs. 56-65: left paramere, lateral view, caudal end to right; Fig. 66: left paramere, mesial view. 54, *P. particeps* (Rincon, Costa Rica); 55, *P. mixtecus* (near Tehuantepec, Mexico); 56, *P. nigrocinctus* (10mi. NW Liberia, Costa Rica); 57, *P. particeps* (Rincon, Costa Rica); 58, *P. peperi* (58a: 3km ENE Chiapa de Corzo, Mexico; 58b: Nueva Ocotepec, Honduras); 59, *P. satanicus* (59a: 3mi. SW Gatun Dam, Panama; 59b: Marajal, Panama); 60, *P. spinicola* (60a: Madden Dam, Panama; 60b: Aracataca, Colombia); 61, *P. mixtecus* (61a: 57.8mi. S Chilpancingo, Mexico; 61b: near Tehuantepec, Mexico); 62, *P. veneficus* (5km E Chamela, Mexico); 63, *P. flavicornis* (63a: Rio Oro, Costa Rica; 63b: 3.6mi. W Choluteca, Honduras); 64, *P. janzeni* (64a: 60mi. SE Acajoneta, Mexico; 64b: 4mi. E San Blas, Mexico); 65, *P. ferrugineus* (65a: Escuintla-Cd. Guatemala, Guatemala; 65b: 10.8mi S Pichucalco, Mexico); 66, *P. ferrugineus* (10.8mi S Pichucalco, Mexico).

absent from the extensor faces of tibiae. Appressed pubescence dense on most of body, including head and abdominal tergite IV. Color varying from light yellow- or orange-brown to black.

Queen diagnosis.—Similar to worker except for caste-specific differences. Larger in size (HW 0.76-1.36, HL 1.05-1.81), head more elongate (CI 0.60-0.80). Ocular indices differing slightly: REL 0.38-0.48, REL2 0.51-0.70. Median clypeal lobe narrower and more protruding, anterior margin convex or straight, laterally rounded or subangulate. Petiole and postpetiole generally more slender (PL/HL 0.57-0.72, PLI 0.43-0.63, PWI 0.47-0.67, PPWI 1.06-1.50). Forewing with 2 cubital cells.

Male, diagnosis.—Head varying from longer than broad to slightly broader than long (CI 0.82-1.04 in a sample of 70 males belonging to all species); compound eye large, prominent (REL2 0.49-0.62). Mandibles with 8+ teeth or denticles on masticatory margin. Palp formula as in females, but somewhat more variable (males with 5p4,3 commoner than in workers or queens). Surface of median clypeal lobe convex, its anterior margin subtriangular in shape (dorsal view) with sides converging medially to a rounded point. Petiole and postpetiole more slender than in workers (PLI 0.40-0.55, PWI 0.35-0.51) and simpler in shape. Posterolateral corners of sternites IV-VIII not notably protruding ventrally. Subgenital plate (sternite IX) with a conspicuous posteromedial concavity (Figs. 54, 55). Posterior margin of pygidium (tergite VIII) convex, directed posteroventrally. Paramere with several characteristic features: a finger-like, posterodorsally directed mediodorsal lobe; angulate or expanded posterodorsal extremity; and mesial dorsoventral ridge which joins the mediodorsal lobe posteriorly. Aedeagus with expanded posterodorsal corner, a medial protrusion on the posterior margin, numerous small teeth (15+) on the posterior margin, and on the outer face a raised ridge curving posterodorsally from a basal origin.

Comments.—Workers and queens of the *P. ferrugineus* group can be distinguished from all other *Pseudomyrmex* by their possession of the following combination of traits: mandibles with 6-7 teeth; palp formula 5,3 or 4,3; standing pilosity common on mesosoma dorsum but absent from

external faces of tibiae; worker metanotal groove conspicuously impressed; and head densely punctulate, sublucid to opaque. The relatively short eyes (worker REL 0.50, queen REL 0.48) and slender petiole (worker PLI 0.71, queen PLI 0.63) are also characteristic. Among the eight other major species groups of *Pseudomyrmex* (diagnosed in Ward, 1989) only the *P. viduus* and *P. oculatus* groups have workers and queens approaching these conditions. Those of the *P. viduus* group have a shinier head, a shorter and more robust petiole (worker PLI > 0.70, worker PWI > 0.70), and standing pilosity on the tibiae (reduced in one species), while workers and queens of the *P. oculatus* group have a palp formula of 6,3 (reduced to 5,3 only in smallest species with worker and queen HW < 0.67), tectiform and sharp-edged median clypeal lobe with a broadly convex margin (dorsal view), elongate eyes (worker REL 0.48-0.61, worker REL2 0.62-0.86, queen REL 0.43-0.57, queen REL2 0.68-0.89), and short petiole (worker PLI 0.67-1.06, queen PLI 0.57-0.94). Among taxonomically isolated species not belonging to one of the major species groups, *P. fervidus* (F. Smith) bears perhaps the closest phenetic resemblance to the *P. ferrugineus* group, but its workers and queens can be distinguished by their shinier and less densely punctulate head, shorter petiole (worker PLI 0.71-0.76, worker PL/HL 0.41-0.44 (n=9); queen PLI 0.65, queen PL/HL 0.49), and standing pilosity on the outer faces of the tibiae. In addition the queens of *P. fervidus* have a distinctive, pointed median clypeal lobe not seen in *P. ferrugineus* group queens.

Males of the *Pseudomyrmex ferrugineus* group can be characterized by their palp formula, medially subangulate clypeal lobe, emarginate subgenital plate, configuration of the paramere, and shape of the aedeagus. They are approached most closely in this combination of traits by males of *P. haytianus* (Forel) and two undescribed Central American species (*P. sp.* PSW-02 and *P. sp.* PSW-54) although, curiously, the workers and queens of those species do not bear a close resemblance to those of the *P. ferrugineus* group.

All species in the *P. ferrugineus* group are obligate inhabitants of Central American swollen-thorn acacias, a biological trait not characterizing any other species group of *Pseudomyrmex*, al-

though a few species in the otherwise quite different *P. gracilis* group and one species in the *P. subtilissimus* group have independently developed an obligate association with the acacias.

Distribution.—Members of the *P. ferrugineus* group are found from eastern (San Luis Potosí, Tamaulipas) and western (Sinaloa) Mexico south through Central America to northern Colombia (Fig. 67). Although no single species spans the entire range of the group, their collective distribution is virtually identical to that of the swollen-thorn acacias (compare Fig. 67 with Janzen 1974:3).

Synonymic List of Species

- P. ferrugineus* (F. Smith 1877) Mexico to Honduras
 = *P. fulvescens* (Emery 1890) (Ward 1989)
 = *P. canescens* (Wasmann 1915) (Ward 1989)
 = *P. wasmanni* (Wheeler 1921) (replacement name for *canescens*)
 = *P. bequaerti* (Wheeler 1942) (Ward 1989)
 = *P. saffordi* (Wheeler 1942) (Ward 1989)
 = *P. vesanus* (Wheeler 1942) (Ward 1989)
 = *P. bequaerti* (Enzmann 1945) (Brown 1949)
 = *P. honduranus* (Enzmann 1945) (Ward 1989)
P. flavicornis (F. Smith 1877) Guatemala to Costa Rica
 = *P. belti* (Emery 1890) (Ward 1989)
 = *P. obnubilus* (Menozi 1927a) (Ward 1989)
 = *P. felloso* (Wheeler 1942) (Ward 1989)
P. janzeni Ward, **sp. nov.** Mexico
P. mixtecus Ward, **sp. nov.** Mexico
P. nigrocinctus (Emery 1890) Guatemala to Costa Rica
 = *P. alfari* (Forel 1906) **syn. nov.**
 = *P. bicinctus* (Santschi 1922) **syn. nov.**
 = *P. peltatus* (Menozi 1927) **syn. nov.**
P. particeps Ward, **sp. nov.** Costa Rica
P. peperii (Forel 1913) Mexico to Nicaragua
 = *P. convarians* (Forel 1913) (Ward 1989)
 = *P. saffordi* (Enzmann 1945) (Ward 1989)
P. spinicola (Emery 1890) Honduras to Colombia
 = *P. atrox* (Forel 1912) **syn. nov.**
 = *P. gaigei* (Forel 1914) **syn. nov.**
 = *P. infernalis* (Wheeler 1942) **syn. nov.**
 = *P. scelerosus* (Wheeler 1942) **syn. nov.**
 = *P. infernalis* (Enzmann 1945) (Brown 1949)
 = *P. scelerosus* (Enzmann 1945) (Brown 1949)
P. satanicus (Wheeler 1942) Panama
P. veneficus (Wheeler 1942) Mexico
 = *P. venificus* (Enzmann 1945) (Brown 1949)

SPECIES ACCOUNTS

Pseudomyrmex ferrugineus (F. Smith 1877)
 (Figs. 18, 27, 65, 66, 70)

Pseudomyrma ferruginea F. Smith 1877:64. Lectotype worker, Mexico (BMNH) [Examined].

Pseudomyrma belti race *fulvescens* Emery 1890:64. Lectotype worker, Guatemala (Beccari) (MCSN) [Examined] [Synonymy by Ward 1989:437; see also Janzen 1967b:391].

Pseudomyrma canescens Wasmann 1915:321. Syntype workers, Tampico, Mexico (Brakhoven) (MCSN, MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma wasmanni Wheeler 1921:92. Replacement name, now unnecessary, for *P. canescens* Wasmann 1915 (nec F. Smith 1877).
Pseudomyrma belti subsp. *bequaerti* Wheeler 1942:164. Lectotype worker, Puerto Castilla, Honduras (J. Bequaert) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *saffordi* Wheeler 1942:162. Lectotype worker, Chicoasen, Chiapas, Mexico (G. N. Collins) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *vesana* Wheeler 1942:163. Holotype (unique syntype) worker, Córdoba, Mexico (F. Knab) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *bequaerti* Enzmann 1945:80. Syntype workers, Puerto Castilla, Honduras (J. Bequaert) (MCZC) [Examined] [Objective synonym of *P. belti bequaerti* Wheeler; Brown 1949:42].

Pseudomyrma kuenckeli var. *hondurana* Enzmann 1945:87. Lectotype worker, Honduras (Bates) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrmex ferruginea [sic] (F. Smith); Janzen 1966:252.

Pseudomyrmex ferrugineus (F. Smith); Kempf

Table 1. Summary of nomenclature used in the biological literature on acacia-ants, *Pseudomyrmex ferrugineus* group.^a For all except some of the most recent (1979-1990) papers, the relationship between the names used in the paper and the species recognized in the current study was established by direct examination of museum specimens collected, or referred to, by the author(s). Only specific and intraspecific epithets are listed since all species were listed in the same genus, *Pseudomyrmex* Guérin, until 1952 when M.R. Smith showed that a different generic name, *Pseudomyrmex* Lund, had priority. By the rules of zoological nomenclature this necessitates a change in the ending of adjectival species names (e.g. *ferruginea* to *ferrugineus*) to agree in gender with *Pseudomyrmex* (masc.) but this convention was not followed by all authors.

Author(s)	Species					
	<i>ferrugineus</i>	<i>flavicornis</i>	<i>nigrocinctus</i>	<i>peperi</i>	<i>spinicola</i>	<i>veneficus</i>
Norton (1868a)	<i>flavidula</i> (part)	—	—	<i>flavidula</i> (part)	—	—
Beli (1874)	—	<i>bicolor</i>	—	—	—	—
Emery (1890,1891)	<i>beli fulvescens</i>	<i>beli</i>	<i>nigrocincta</i>	—	<i>spinicola</i>	—
Wheeler (1913)	<i>beli fulvescens</i> (part)	<i>beli</i> (part)	<i>nigrocincta</i>	—	<i>spinicola</i> (part)	<i>beli</i> (part)
	<i>spinicola</i> (part)				<i>beli fulvescens</i> (part)	
Wasmann (1915,1916)	<i>conescens</i>	<i>beli</i>	<i>nigrocincta</i>	—	<i>spinicola</i>	—
Safford (1922)	<i>beli fulvescens</i> (part)	<i>beli</i>	<i>nigrocincta</i>	<i>beli "varieties"</i> (part)	<i>spinicola</i>	<i>beli fulvescens</i> (part)
Menozzi (1927a,b)	—	<i>beli obtusula</i>	<i>peltata</i>	—	—	—
Skwarra (1934a,b)	<i>beli wasmanni</i> (part)	—	—	<i>beli wasmanni</i> (part)	—	—
Wheeler (1942)	<i>beli fulvescens</i>	<i>beli</i>	<i>nigrocincta</i>	<i>spinicola convarians</i>	<i>spinicola</i>	<i>beli venefica</i> (part)
	<i>beli saffordi</i> (part)	<i>beli felloso</i>	<i>peltata</i>	<i>beli saffordi</i> (part)	<i>spinicola atrox</i>	
	<i>beli vesana</i>	<i>beli obtusula</i>			<i>spinicola gagei</i>	
	<i>beli boquerii</i>				<i>spinicola infernalis</i>	
	<i>beli wasmanni</i>				<i>spinicola sclerosa</i>	
Janzen (1966,1967a)	<i>ferruginea spinicola</i> (part)	<i>beli</i> (part)	<i>nigrocincta</i> (part)	<i>nigrocincta</i> (part)	<i>spinicola</i> (part)	<i>beli</i> (part)
Janzen (1967b, 1969, 1973, 1974, 1975, 1983)	<i>ferruginea</i> (part)	<i>beli</i> (part)	<i>nigrocincta</i> (part)	<i>nigrocincta</i> (part) and "undescribed sp."	<i>ferruginea</i> (part)	<i>venefica</i>
Hölldobler & Engel (1979), Hölldobler & Engel-Siegel (1985)	—	—	—	—	<i>ferruginea</i>	—
Mintzer (1982), Mintzer & Vinson (1985), Mintzer et al. (1987)	<i>ferruginea</i>	—	—	—	—	—
Errard (1984)	<i>ferruginea</i>	—	—	—	—	—
Espele & Hermann (1988)	<i>ferrugineus</i>	—	—	—	—	—
Ward (1989)	<i>ferrugineus</i>	<i>flavicornis</i>	<i>nigrocinctus</i>	<i>peperi</i>	<i>spinicola</i>	<i>veneficus</i>
Young et al. (1990)	—	<i>flavicornis</i>	<i>nigrocinctus</i>	—	<i>spinicola</i>	—

^aOf the four other species in the *P. ferrugineus* group, *P. sataninus* has always been correctly identified (Wheeler, 1942; Janzen, 1969, 1973, 1974); *P. mixticus* was mistaken for *P. veneficus* by Wheeler (1942) and for *P. flavicornis* (= *beli*) by Janzen (1966, 1973); *P. janzeni* was referred to by Janzen (1973, 729) as an undescribed species derived from *P. ferrugineus*; and *P. parvicornis* has received no mention in the literature.

1972:218.

Worker measurements (n=69).—HL 0.99-1.33, HW 0.92-1.15, MFC 0.054-0.108, CI 0.81-0.94, REL 0.42-0.48, REL2 0.48-0.54, OOI 1.39-3.16, VI 0.60-0.78, FCI 0.054-0.101, SI 0.41-0.46, SI2 0.79-0.91, NI 0.61-0.72, PLI 0.54-0.69, PWI 0.56-0.73, PPWI 1.34-1.70.

Worker diagnosis.—Medium-sized species (HW > 0.91; LHT 0.75-1.06) with broad head (CI > 0.80); anterior margin of median clypeal lobe straight or weakly concave, rounded laterally; palp formula 5.3; frontal carinae well separated (FCI > 0.05) and median lobe of antennal sclerite not strongly exposed (FCI2 0.45-0.69); mesosomal profile typically as in Fig. 27, with mesonotum notably inclined and with basal face of propodeum rounding gradually into declivitous face, but deviations from this pattern occur; petiole relatively short, high and wide (see relevant metrics: PLI, PWI), with a distinct anterior peduncle (PWI3 0.36-0.50); posterolateral angles of petiole moderately developed but not as pronounced as in *P. peperii* (compare Figs. 24 and 27); postpetiole broad. Head densely punctulate, predominantly opaque or subopaque but at least weakly shining on upper third of head between ocelli and compound eye; mesosoma punctulate to punctulate-coriaceous, subopaque to sublucid; posterior portions of propodeum opaque to subopaque and usually overlain by larger but weak, irregular punctures or rugulae. Petiole, postpetiole and gaster with fine piligerous punctures, sublucid. Standing pilosity common; pubescence dense but fine and appressed on most surfaces. Color variable, from light reddish- or yellowish-brown to very dark brown, gaster (and usually head) somewhat darker than the mesosoma; mandibles, scapes, fronto-clypeal complex, and apices of legs usually lighter.

Comments.—Workers and queens of *P. ferrugineus* can be recognized by features of head morphology (laterally rounded median clypeal lobe, well separated frontal carinae and correspondingly limited exposure of the median lobes of the antennal sclerites, and moderately broad worker head; see Fig. 18), head sculpture (densely punctulate and (sub)opaque, but weakly shining on upper third of head between the ocelli and compound eye), and coloration (variably brown, not black or orange-

brown). This species is most likely to be confused with the allopatric *P. janzeni* and the partly sympatric *P. flavicornis*. See under those species for more specific discussion.

Distribution and biology.—*P. ferrugineus* is distributed from eastern and southern Mexico to El Salvador and Honduras (Fig. 70). It is a common species and colonies have been recorded from all swollen-thorn acacia species growing within its range, i.e. *Acacia chiapensis*, *A. collinsii*, *A. cookii*, *A. cornigera*, *A. gentlei*, *A. globulifera*, *A. hindsii*, *A. janzenii*, *A. mayana* and *A. sphaerocephala*. *P. ferrugineus* is usually monogynous (Janzen 1967b, 1973) but a few alcohol nest series from Guatemala, belonging to apparently mature colonies (as judged by the presence of alates), contained more than one dealate queen. Janzen (1966, 1967b) conducted a massive experimental study of the interaction between *P. ferrugineus* and *Acacia cornigera* in Mexico, and the results of these experiments, together with copious additional observations by Janzen, showed conclusively that the ants protect the acacia from herbivores and competing plants (especially vines). *P. ferrugineus* was also the subject of a study on kinship and nestmate recognition among workers (Mintzer 1982; Mintzer et al. 1985) which demonstrated a worker-based and probably inherited component to colony odor. Statements about the biology of "*P. ferruginea*" from regions south of El Salvador and Honduras (e.g. Janzen 1983) refer to a different species, *P. spinicola*.

Material examined (AMNH, BMNH, CASC, CHAH, CISC, CUIC, INHS, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMV, PSWC, SEMC, UCDC, USNM, WPMC).—

BELIZE Belize: 2.2mi W Belize, rd.to Chetumal (D.H.Janzen); 3.8mi NW Belize, rd.to Chetumal (D.H.Janzen); 4.9mi SW Belize, rd.to Cayo (D.H.Janzen); Belize (Baker; c.u.); Manatee [River] (J.D.Johnson; c.u.); nr. Belize (N.L.H.Krauss); Cayo: 36.1mi SW Belize (D.H.Janzen); 36.1mi [S]W Belize (U.Kansas Mex.Exped.); El Cayo [=San Ignacio] (N.L.H.Krauss); Pine Mtn. Ridge, Mecal R., 415m (G.D.Alpert); San Ignacio (S.E.Schoenig); Corozal: 13.5mi S Sta.Elena (Louisville) (D.H.Janzen); 15mi S Sta.Elena (Louisville) (D.H.Janzen); Orange Walk: 5mi SE Orange

Walk, rd.to Belize (D.H.Janzen); Toledo: Punta Gorda (H.Broomfield).

EL SALVADOR *Chalatenango*: 4.7mi NW La Palma, 880m (D.H.Janzen); 5.5mi SE La Palma, 1130m (D.H.Janzen).

GUATEMALA *Alta Verapaz*: San Joaquín, nr. San Cristóbal Verapaz, 1080m (D.H.Janzen); Trece Aguas (Schwarz & Barber); *Chimaltenango*: Yepocapa (H.T.Dalmat); *Cotepeque*: 2mi W Cotepeque (D.H.Janzen); *El Progreso*: 4.9mi SW Sanarate, 780m (D.H.Janzen); *Escuintla*: 1.7mi S Escuintla, 370m [on CA-2] (D.H.Janzen); 12.6mi NE Escuintla, rd. to Cd. Guatemala, 1120m (D.H.Janzen); 15km E Escuintla [on CA-9] (D.H.Janzen); 3mi N Escuintla [on CA-9] (D.H.Janzen); 3mi S Escuintla [on CA-9] (D.H.Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H.Janzen); 6.8mi S Escuintla, 280m [on CA-2] (D.H.Janzen); 8.3mi N Escuintla [on CA-9] (D.H.Janzen); 9.2mi N Escuintla, 900m [on CA-9] (D.H.Janzen); Escuintla (W.M.Wheeler); Pantaleon (Champion); *Guatemala*: 16.2mi NE Cd. Guatemala (D.H.Janzen); 19km S Cd. Guatemala [on CA-9] (D.H.Janzen); 20mi SE Cd. Guatemala, 1060m [on CA-1] (D.H.Janzen); 6.2mi NE Cd. Guatemala, 700m (D.H.Janzen); 7.9mi S Cd. Guatemala, 1360m [on CA-9] (D.H.Janzen); 8.1mi NE Cd. Guatemala, 850m (D.H.Janzen); Cd. Guatemala (Champion); Cd. Guatemala, 980m (D.H.Janzen); Escuintla-Cd. Guatemala [=19km S Cd. Guatemala] (D.H.Janzen); *Huehuetenango*: 12.4mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 12.5mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 37.6mi NW Huehuetenango, 900m (D.H.Janzen); 7.1mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 9.3mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); *Izabal*: 1.1mi NE Quiriguá, 120m (D.H.Janzen); 2.1mi SW Morales, 50m (D.H.Janzen); Lago Izabal, 1km NE El Estor [=1.5km NE El Estor] (D.H.Janzen); Los Amates (Kellerman); Murciellago (D.H.Janzen); Quiriguá (W.M.Wheeler); *Jutiapa*: 6.7mi N San Cristóbal, 280m (D.H.Janzen); 6.9mi N San Cristóbal, 290m (D.H.Janzen); 9mi SW Jutiapa, 950m (D.H.Janzen); *Petén*: 70km NW Tikal (W.R.Tschinkel); Tikal (T.H.Hubbell); N.L.H.Krauss; W.R.Tschinkel; *Quezaltenango*: 7.2mi NE San Felipe, on

Retalhuleu-Quezaltenango Rd. (D.H.Janzen); 7.5mi NE San Felipe, on Retalhuleu-Quezaltenango Rd. (D.H.Janzen); *Retalhuleu*: 1.3mi E Champerico (D.H.Janzen); 2mi NE Champerico (D.H.Janzen); 5mi W Retalhuleu (D.H.Janzen); 5mi W Retalhuleu, Hwy. CA-2, at Rio Nil (D.H.Janzen); Champerico (Baker; F.Knab); Puente Samala, 3.8mi NE San Felipe (D.H.Janzen); Retalhuleu (Stoll); *Santa Rosa*: 25mi SE Escuintla, 200m [on CA-2] (D.H.Janzen); *Solola*: "Pacific slope", 3000ft. (c.u.); *Suchitepéquez*: Patulul (W.M.Wheeler); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.6mi SW El Lobo, 100m [on CA-9] [=16.6mi NE Piedras de Afilar] (D.H.Janzen); 8.1mi SW Los Amates, 160m [on CA-9] [=8.0mi NE El Lobo] (D.H.Janzen); 8.2mi NE Piedras de Afilar, 160m [on CA-9] [=12.2mi NE Rio Hondo] (D.H.Janzen); *dept.unknown*: "Guatemala" (Beccari); Concepcion, 1400ft. (C.N.Ainslie); Mimosa, "Cocepcion" [Concepcion] (C.N.Ainslie).

HONDURAS *Atlántida*: Tela (quarantine New Orleans, U.S.A.) (T.J.Baker); *Colón*: Puerto Castilla (J.Bequaert); *Comayagua*: "Comayaena" (S. Passoa); 11.7mi S San Antonio, 830m (D.H.Janzen); 15.7mi N Siguatopeque, 530m (D.H.Janzen); Minas de Oro (J.B.Edwards); *Copán*: 10.4mi S Sta. Rosa de Copán, 980m (D.H.Janzen); 11.9mi S Sta. Rosa de Copán, 1130m (D.H.Janzen); 17.3mi N Sta. Rosa de Copán, 780m (D.H.Janzen); *Cortés*: 24.6mi SW San Pedro Sula, 240m (D.H.Janzen); 6.8mi S San Pedro Sula, 480m [=20.9mi SW Quimistán] (D.H.Janzen); San Pedro Sula (S.C.Bruner; W.M.Mann); *Ocatepeque*: 4.4mi E [Nueva] Ocatepeque, 1310m (D.H.Janzen); *Santa Bárbara*: 7.3mi E Quimistán (D.H.Janzen); 13.7mi SW Quimistán, 320m (D.H.Janzen); *Yoro*: Coyoles, W of Olanchito (Echternacht); *dept.unknown*: "Honduras" (Bates).

MEXICO *Campe*: 0.1mi S Tenabo (D.H.Janzen); 0.8mi E Campeche (D.H.Janzen); 10.6mi E Campeche (D.H.Janzen); 20mi E Campeche, Hwy. 180 (D.H.Janzen); 29mi E & 12mi S Campeche (Ruinas Edzna) (D.H.Janzen); 48mi NE Puerto Real (Isla Aguada), Hwy. 180 (D.H.Janzen); Ruinas Edzna (U.Kansas Mex.Exped.); *Chis.*: 10 mi NE [NW?] Tapachula [on Hwy. 200?] (D.H.Janzen);

10.8mi S Pichucalco (D.H.Janzen); 11km SE Pichucalco, 400m (P.S.Ward); 11mi E Arriaga (D.H.Janzen); 1km WSW Palenque, 80m (P.S.Ward); 26km E Cintalpa (W.MacKay); 2mi S Pichucalco (D.H.Janzen); 32mi W [San] Cristóbal de las Casas, Hwy.190 (D.H.Janzen); 3km ENE Chiapa de Corzo, 500m (P.S.Ward); 3mi N Soyalo [on Hwy.195] (D.H.Janzen); 4mi NW Ocosingo (R.C.Bechtel & E.I.Schlinger; R.F.Smith); 4mi S Simojovel (R.C.Bechtel & E.I.Schlinger; E.I.Schlinger); 56.9mi NE [NW?] Tapachula [on Hwy.200?] (D.H.Janzen); 5mi SE Tapilula [on Hwy.195] (D.H.Janzen); 6.9mi N Tapilula (D.H.Janzen); 7mi SW Teapa [on Hwy.195] (D.H.Janzen); 8.5mi S La Trinitaria, 1160m (U.Kansas Mex.Exped.); 8.5mi S La Trinitaria, Hwy.190 (D.H.Janzen); 8mi W Las Cruces, Hwy.190, 660m (D.H.Janzen); 96km S Tuxtla Gutiérrez, 732m (D.E. & J.A.Breedlove); Acapetahua Las Bugamillas (F.Díaz); Arriaga (D.H.Janzen); Cd. Cuauhtemoc (D.H.Janzen); Chicoasen (G.N.Collins); El Real (Goodnight & Stannard); Ixtacomitan (R.Andrews); Llano Grande (G.N.Collins); Palenque (c.u.); Pichucalco (G.N.Collins); San Huixtla, Huixtla (J.G.Pereira); Ruinas Palenque (E.M.Fisher); San Sebastian [near Tuxtla Gutierrez; see Safford 1922:393] (G.N.Collins); Santo Domingo, 15mi SE [SW?] Simojovel (R.F.Smith); Tapilula (D.H.Janzen); Tonalá, 40m (D.H.Janzen); Tonala [prob.=Tonalá] (A.Petrunkewitch); Tuxtla Gutierrez (N.L.H.Krauss; W.P.Stoutamize); Yaxoquintela (J.E.Rawlins); Yerba Santa (G.N.Collins); *Gro.*: 10mi NE Acapulco (D.H.Janzen); 15.8mi S Chilpancingo (D.H.Janzen); 18mi S Chilpancingo (F.D.Parker; F.D.Parker & L.A.Stange); 25.4mi S Chilpancingo (D.H.Janzen); 55mi N Acapulco, Hwy.95 (Cornell Univ.Mex.Field Party; c.u.); 57.8mi S Chilpancingo (D.H.Janzen); 59.9mi N Acapulco (D.H.Janzen); 62.4mi N Acapulco (D.H.Janzen); 74km N Acapulco (W.MacKay); Acapulco (L.J.Lipovsky); Revolcadero (N.L.H.Krauss); San Geronimo de Juarez (W.von Hagen); *Hgo.*: 2km W Orizatlán, 245m (W.MacKay); *Mor.*: 15mi S Cuernavaca (E.S.Ross; W.S.Ross); Cuernavaca (W.M.Wheeler); *Oax.*: 11.4-17.0mi W Tehuantepec (D.H.Janzen); 1mi W Temascal (D.H.Janzen); 22.2mi N Puerto Escondido, 700m (D.H.Janzen); 25mi W Tehuantepec (D.H.Janzen); 3.2mi NE Tehuantepec (D.H.Janzen); 42km N San Pedro Pochutla, 850m (W.MacKay); 44mi W Tehuantepec (E.E.Gilbert & C.D.MacNeil); 5mi E Temascal (D.H.Janzen); 9.6km E Santiago Astata, 10m (W.MacKay); Bahías de Huatulco (W.MacKay); Pinotepa Nacional (S.W.T.Batra); Salina Cruz (D.H.Janzen); Tehuantepec (F.Knab; W.P.Stoutamize); Temascal (H.V.Daly; D.H.Janzen); Temascal, 25m (D.H.Janzen); Tuxtepec (J.Camela G.; W.M.Mann); Valle Nacional (G.V.Halfpiter); *Q.Roo.*: 12.2mi S Peto, Q.Roo-Yucatan border (D.H.Janzen); 16.9mi W Cd. Chetumal, rd. to Peto (D.H.Janzen); 22.5mi S Felipe Carillo Puerto (D.H.Janzen); 6.4mi E Polyuc (D.H.Janzen); 7mi W Felipe Carillo Puerto (D.H.Janzen); 8.1mi S Felipe Carillo Puerto (D.H.Janzen); 8mi S Felipe Carillo Puerto (D.H.Janzen); Sian Ka'an (A.Dejean); Sian Ka'an Reserve, nr. Felipe Carillo Puerto (A.Dejean); Vallarta (A.Dejean); *S.L.P.*: 27mi N Tamazunchale (D.H.Janzen); 40-50mi NW Cd. del Maíz (W.S.Ross); 4mi N Valles, 300ft. (W.S.Creighton); Cd. Valles (D.H.Janzen); El Bonito, 7mi S Cd. Valles, 300ft. (P.H. & M.Arnaud); El Salto (A.Mintzer; c.u.); Huichihuayan (L.J.Lipovsky); Río Amahac, Tamazunchale, 300ft. (W. S. Creighton); Tamazunchale (D. H. Janzen; W. S. Ross); locality not specified, prob. Tanquian [see Safford 1923:390] (Safford); *Tab.*: 0.6mi S Paraíso on rd. to Cárdenas (D.H.Janzen); 0.9mi S Chontalpa (D.H.Janzen); 12.8mi S Chontalpa (D.H.Janzen); 2.1mi E Frontera (D.H.Janzen); 3 mi W Cárdenas (D.H.Janzen); 30.2mi W Cd. El Carmen (D.H.Janzen); 37.8mi E Coatzacoalcas, Hwy.180 (D.H.Janzen); 6.6mi S Chontalpa (D.H.Janzen); Chontalpa, 26mi S Cárdenas (D.H.Janzen); Cárdenas (D.H.Janzen); Teapa (J.C. & D.Pallister; H.H.Smith; W.P.Stoutamize); *Tamps.*: 22.7mi S Cd. Victoria (D.H.Janzen); 41mi S Cd. Victoria (C.W.Obrien); 50mi N Valles (G.E.Bohart); 5mi N Cd. Mante (A.Mintzer); 7km WSW El Encino, 140m (P.S.Ward); Antiguo Morelos (c.u.); Cd. Madero (F.Infante M.); Ciudad Mante (N.E. & M.A.Evans; N.L.H.Krauss); El Limón (H.E.Evans); Forlón (L.J.Lipovsky); Gonzales (c.u.); Llera (W.E.LaBerge); Mesa de Llera (A.Mintzer); N of Antiguo Morelos (A.Mintzer); Río Guayalejo at

Hwy.85 (A.S.Menke & L.A.Stange); S of Cd. Mante (A.Mintzer); Tampico (Brakhoven; D.L.Crawford; H.Jourdan; N.L.H.Krauss; Locke; E.Palmer; E.A.Schwarz; W.P.Stephen; c.u.); Tampico, dunes at Cd. Madero (D.H.Janzen); Xicotencatl (H.C.Millender); *Ver.*: "N.M..Vera Cruz" (Townsend); "Vera Cruz" (G.Seurat; H.H.Smith); 10mi W Veracruz (G.E.Bohart); 14km ENE La Tinaja, 50m (P.S.Ward); 15mi W Veracruz (U.Kansas Mex.Exped.); 16km E Cuilahuac [=Cuicilahuac] (W.MacKay); 24.9mi NW Acayucan (D.H.Janzen); 28km N Cardel, Morro de la Mancha (V.Rico-Gray); 30mi S Acayucan (F.D.Parker); 3mi N Sayula (R.C.Bechtel; R.C.Bechtel & E.I.Schlenger); 4mi NE Minatitlan (R.C.Bechtel & E.I.Schlenger); 4mi NW Rinconada Antigua, 1350ft. (U.Kansas Mex.Exped.); 4mi W Puente Nacional, 900ft. (U.Kansas Mex.Exped.); 6.5km N Tierra Blanca, 50m (W.MacKay); 7mi S Cardel, 600ft. (c.u.); 9km NNW Sontecomapan, 20m (P.S.Ward); Boca del Rio (U.Kansas Mex.Exped.); Buen Pais (R.C.Bechtel & E.I.Schlenger); Camaron (E.Skwarra); Cordoba (F.Knab; R.R.Snelling; c.u.); Cotaxtla Exp. Sta., Cotaxtla (D.H.Janzen); Est. Biol. Los Tuxtlas (H.A.Hespenheide); Est. Biol. "Los Tuxtlas", nr. San Andres Tuxtla (G.Ibarra M.); Fortin (c.u.); Jalapa (Rangel; W.M.Wheeler; c.u.); Jalapilla, mun. Jilotepec (G.Alemán); Los Cocos (A.Petrunkewitch); Los Tuxtlas, 10km NNW Sontecomapan, 200m (P.S.Ward); Mirador (E.Skwarra); Mocambo (D.H.Janzen); Orizaba (c.u.); Palma Sola (Halferty & Reyes); Panuco (F.Parker & D.Miller); Playa Azul, Catemaco (W.P.Stoutamize); Pueblo Nuevo, nr. Tezonapa (Cornell Univ. Mex. Field Party); Remutadero (E.Skwarra); Santa Lucrecia [=Jesus Carranza] (F.Knab; P.Knab); Tamarindo (E.Skwarra); Tamos (F.C.Bishop); Tinajas [presumably La Tinaja, on Hwy.150] (F.D.Parker & L.A.Stange); Tlacocintla (E.Skwarra); Veracruz (G.E.Bohart; N.L.H.Krauss; E.Skwarra; L.A.Stange); *Yuc.*: 14.8mi S Ticul, "Hwy.180" [prob.Hwy.261] (D.H.Janzen); 8mi E Merida (rd. to Pto. Juarez) (D.H.Janzen); Merida (D.H.Janzen; N.L.H.Krauss); Merida (S margin of town) (D.H.Janzen); Tekax, 33mi W Peto (D.H.Janzen); Temax (Gaumer); *state unknown*: "Mex" ("Norton").

***Pseudomyrmex flavicornis* (F. Smith 1877)**
(Figs. 16, 25, 63, 69)

Pseudomyrma flavicornis F. Smith 1877:67. Lectotype worker, Nicaragua (BMNH) [Examined].

Pseudomyrma belti Emery 1890:63. Syntype workers, Alajuela, Costa Rica (BMNH, MCSN) [Examined] [Synonymy by Ward 1989:438].

Pseudomyrma belti var. *obnubila* Menozzi 1927a:273. Syntype worker, San José, Costa Rica (H. Schmidt) (NHMB) [Examined] [Synonymy by Ward 1989:438].

Pseudomyrma belti subsp. *felloso* Wheeler 1942:160. Syntype workers, Nicaragua (W. Fluck); Granada, Nicaragua (C. F. Baker) (AMNH, LACM, MCZC) [Examined] [Synonymy by Ward 1989:439].

Pseudomyrmex flavicornis (F. Smith); Kempf 1972:218.

Worker measurements (n=29).—HL 1.06-1.42, HW 0.99-1.21, MFC 0.075-0.114, CI 0.83-0.94, REL 0.39-0.45, REL2 0.45-0.51, OOI 1.28-2.71, VI 0.59-0.73, FCI 0.068-0.098, SI 0.40-0.46, SI2 0.82-0.97, NI 0.61-0.68, PLI 0.57-0.67, PWI 0.60-0.72, PPWI 1.36-1.80.

Worker diagnosis.—Similar to *P. ferrugineus* (q.v.) except as follows. Larger, with shorter eyes, on average (Figs. 16, 50). Head densely punctulate, opaque; overlying rugulo-punctate sculpture on propodeum tending to be better developed than in *P. ferrugineus*. Pilosity and pubescence denser on average. Head black, gaster and postpetiole dark brown to black, mesosoma and petiole varying from black to a contrasting lighter brown or reddish-brown; mandibles, scapes, fronto-clypeal complex, and apices of legs brown.

Comments.—Key traits of this species are the laterally rounded median clypeal lobe, large size (worker HW > 0.98; queen HW 1.12-1.19, n=13), broad opaque head (worker CI > 0.82; queen CI 0.73-0.76) and dark color. *P. flavicornis* is one of three species in the *P. ferrugineus* group whose workers and queens have a black or very dark brown body (mesosoma sometimes contrastingly lighter). The other two, *P. mixtecus* and *P. veneficus*, are allopatric to *P. flavicornis* and smaller in size;

other distinguishing features are mentioned in the key and discussed under those species. A tendency towards lighter coloration of the mesosoma in northern populations of *P. flavicornis* sometimes makes it difficult to distinguish this species from sympatric dark-colored *P. ferrugineus*. Even the darkest workers and queens of the latter species are, however, smaller (an average difference in workers, almost absolute in *P. ferrugineus* queens which have HW 0.96-1.12 ($n = 37$)) with longer eyes (Fig. 50) and shorter scapes for a given relative head breadth (Fig. 51); and they show some reflectance of light on the upper third of the head between the ocelli and compound eye in contrast to the more or less opaque-headed *P. flavicornis*. In addition, *P. ferrugineus* queens have more elongate heads (CI 0.68-0.73) than those of *P. flavicornis*.

Distribution and biology.—This is a monogynous species ranging from Guatemala to Costa Rica (Fig. 69), which inhabits *Acacia collinsii* and, less frequently, *A. cornigera* and *A. hindsii*. It was one of the first acacia-ants to be brought to the attention of naturalists, thanks to an early account of its biology by Thomas Belt (1874) (under the name *Pseudomyrma bicolor*). In the more recent literature *P. flavicornis* has usually been referred to as "*P. belti*", but note that there is not a perfect correspondence in name usage (Table 1).

Material examined (AMNH, ANSP, BMNH, CASP, CUIC, INBC, LACM, MCSN, MCZC, MZSP, NHBM, NHMV, PSWC, SEMC, UCDC, USNM).—

COSTA RICA *Alajuela*: Alajuela (A.Alfaro); Atenas (A.Alfaro); Ojo de Agua (A.Alfaro); Tacares (A.Alfaro); Turrúcares (A.Alfaro); *Guanacaste*: 1.4mi N La Cruz, 200m (D.H.Janzen); 10.7mi NW Liberia (D.H.Janzen); 1km S Cañas (D.H.Janzen); 2mi E Playa Coco (D.H.Janzen); 2mi SE Cañas [=2mi S Cañas] (D.H.Janzen); 4km S Cañas (D.H.Janzen); 5km S Liberia (D.H.Janzen); 6mi E, 6mi S Cañas (D.H.Janzen); 6mi W Liberia (D.H.Janzen); 7km N Cañas (D.H.Janzen); Bahía del Coco (A.Alfaro); Ballena, Rio Tempisque (A.Alfaro); El Coco (R.J. Hampton); Finca Taboga, 6mi S, 6mi W Cañas (D.H.Janzen); Hda. La Pacifica, 5km NW Cañas (E.R. Heithaus); Hda. La Pacifica, nr. Cañas, 50m (P.S. Ward); La Cueva, 12km N Liberia (D.H.Janzen); Liberia (A.Alfaro);

M.G. Naumann); Palo Verde (D.E. Gill); H.A. Hespeneheide; D.H. Janzen; D. Whitacre); Palo Verde, 50m (D.M. Olson); Palo Verde, <100m (J. Longino); Rio Corobici, nr. Cañas (R.M. Bohart); Santa Cruz (P.P. Calvert); Santa Rosa Natl. Pk. (F. Joyce); Santa Rosa Natl. Pk., 300m (J. Longino); P.S. Ward); Santa Rosa Natl. Pk., 5m (P.S. Ward); Santa Rosa Natl. Pk., <5m (P.S. Ward); Tempisque (A. Alfaro); *Heredia*: Lagunilla (C.H. Ballow); *Puntarenas*: 1km NE Tárcoles, 20m (P.S. Ward); 4km E Tivives, 5m (L.S. Farley); Barranca, near Puntarenas (A. Alfaro); *San José*: Bebedero (A. Alfaro); Rio Oro (D.H. Janzen); San José (Nauck; H. Schmidt); Villa Colon (A. Alfaro); Villa Colon, 600-700m (J. Longino); *prov. unknown*: "Costa Rica" (c.u.); Cimela (J.F. Tristan).

EL SALVADOR *Ahuachapán*: 7.8mi S Hachadura, 50m (D.H. Janzen); *Chalatenango*: 5.4mi N La Palma, 850m (D.H. Janzen); *La Libertad*: 2.6mi S Santa Tecla, 1010m [=11.8mi N La Libertad] (D.H. Janzen); 2mi E La Libertad (D.H. Janzen); La Libertad (E.S. Ross); Quezaltepeque (D. Cavagnaro & M.E. Irwin); *La Unión*: 7.1mi W Amatillo, 190m (D.H. Janzen); *Lapa*: 11.6mi W Zacatecoluca, 0m (D.H. Janzen); *San Miguel*: 0.4mi W San Miguel (D.H. Janzen); betw. La Unión & San Miguel, 110m (D.H. Janzen); *San Salvador*: San Salvador (O.L. Cartwright; N.L.H. Krauss); *Sonsonate*: 34.4mi W La Libertad (D.H. Janzen); 6.6mi S Sonsonate [=43.6mi W La Libertad] (D.H. Janzen); *Usulután*: E slope Cerro Verde, 3800ft. (D.Q. Cavagnaro & M.E. Irwin); *dept. unknown*: Los Chorros (D.Q. Cavagnaro & M.E. Irwin); Los Chorros Natl. Pk. (M.E. Irwin).

GUATEMALA *Escuintla*: 12.6mi NE Escuintla, rd. to Cd. Guatemala, 1120m (D.H. Janzen); 15km E Escuintla [on CA-9] (D.H. Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H. Janzen); *Guatemala*: 19km S Cd. Guatemala [on CA-9] (D.H. Janzen); 7.9mi S Cd. Guatemala [on CA-9] (D.H. Janzen); Amatitlán (Bates); Escuintla-Cd. Guatemala [=19km S Cd. Guatemala] (D.H. Janzen); Lake Amatitlán (c.u.); *Jutiapa*: 47mi S Escuintla, 250m [=47mi SE Escuintla] (D.H. Janzen); 7.7mi E Jutiapa, Hwy. 1, 900m (D.H. Janzen); 9.7mi E Jutiapa, 750m (hwy. to San Cristóbal) [=9.3mi NE Jutiapa] (D.H. Janzen); *Santa Rosa*: 12.2mi W Taxisco (D.H. Janzen); 3.8mi S

Guazacapán (D.H.Janzen); Guazacapán (R.H.Painter); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.6mi SW Rio Hondo, 200m [on CA-9] (D.H.Janzen); 22.3mi SW Quiriguá [on CA-9] (D.H.Janzen); 22.3mi SW Quiriguá [on CA-9] (D.H.Janzen); 8.2mi NE Piedras de Afilar, 160m [on CA-9] [=12.2mi NE Rio Hondo] (D.H.Janzen); km142 on Guatemala-Pto. Barrios Rd. nr. Los Amates (D.H.Janzen).

HONDURAS *Choluteca*: 19mi NE Choluteca (D.H.Janzen); 3.6mi W Choluteca, 200m (D.H.Janzen); 4.5mi W Choluteca (D.H.Janzen); *Colón*: Puerto Castilla (J.Bequaert); Valle: 4.6mi E Jicaro Galan, 190m (D.H.Janzen); La Union, 28.4mi E El Amatillo (frontera) (D.H.Janzen).

NICARAGUA *Chontales*: no specific locality (T.Belt); *Estelí*: 2mi N Condega, 500m (D.H.Janzen); *Granada*: 2.2mi W Nandaime (D.H.Janzen); 2mi N Nandaime, 160m (D.H.Janzen); Granada (C.F.Baker); *León*: 28.1mi SE León (D.H.Janzen); *Managua*: 8.1mi E San Benito (D.H.Janzen); 8.8mi N Tipitapa (D.H.Janzen); 9.9mi NE Masachapa, Hwy. 8, 180m (D.H.Janzen); 9mi N Tipitapa, 50m (D.H.Janzen); *Matagalpa*: 15.8mi NW Sebaco [=15.8mi W Sebaco] (D.H.Janzen); 2.6mi N Dario (D.H.Janzen); 4.1mi S Matagalpa, 650m (D.H.Janzen); 4.5mi SE Dario (D.H.Janzen); *Rivas*: 1mi N San Juan del Sur (D.H.Janzen); 1mi NW Peñas Blancas [=1mi N Peñas Blancas] (D.H.Janzen); 20.5mi NW Peñas Blancas (D.H.Janzen); 4.4mi SE La Virgen [=4.4mi S La Virgen] (D.H.Janzen); Isla Ometepe (F.Joyce); La Virgen [on Hwy. 1] (D.H.Janzen); San Juan del Sur, 10m (D.H.Janzen); *Zelaya*: Wounta Hanlover (Fluck); *dept.unknown*: "Nicaragua" (W.Fluck; c.u.).

***Pseudomyrmex janzeni* Ward, sp. nov.**

(Figs. 19, 29, 64, 70)

Holotype worker.—MEXICO, Nayarit: 60 mi. SE Acaponeta, Hwy. 15, 15.ix.1963, D. H. Janzen (LACM). HW 1.00, HL 1.08, EL 0.51, PL 0.55, PH 0.36.

Paratypes.—Same data as holotype: series of 166 workers, 62 queens and 45 males (AMNH,

BMNH, CASC, EBCC, GBFM, INBC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material is listed below.

Worker measurements (n=12).—HL 1.00-1.18, HW 0.93-1.03, MFC 0.063-0.096, CI 0.88-0.94, REL 0.45-0.47, REL2 0.49-0.52, OOI 1.45-2.29, VI 0.58-0.68, FCI 0.068-0.098, SI 0.42-0.45, SI2 0.84-0.91, NI 0.62-0.69, PL1 0.59-0.71, PW1 0.63-0.73, PPW1 1.37-1.73.

Worker diagnosis.—Very similar to *P. ferrugineus* (q.v.) except as follows. Size smaller, on average. In lateral view mesonotum less steeply inclined; basal and declivitous faces of propodeum forming a less obtuse angle (compare Figs. 27 and 29). Petiole shorter and higher, on average (Fig. 48). Weak rugulo-punctate sculpture on propodeum even less evident than in *P. ferrugineus*. Pubescence denser, becoming decumbent to suberect on parts of body, most notably the gula (Fig. 19). Head and mesosoma rather light orange-brown, gaster the same or a slightly darker brown.

Comments.—Within the *P. ferrugineus* group *P. janzeni* can be characterized by its relatively small size (worker and queen HW < 1.04), broad head (worker CI > 0.86), laterally rounded median clypeal lobe, and uniform orange-brown color. *P. janzeni* is evidently closely related to *P. ferrugineus* (as surmised by Janzen 1973); all of the metric measurements and indices of these two species overlap, although there is a tendency for *P. janzeni* workers to have shorter, higher petioles (Fig. 48). Workers and queens of *P. janzeni* are perhaps best distinguished from those of *P. ferrugineus* by the combination of lighter orange-brown color, suberect gular pubescence (best seen in a backlit lateral view of the head), and the flatter profile of the worker mesosoma (see description above and Fig. 29). While some individuals of the highly variable *P. ferrugineus* approach these conditions there is no indication of a convergence towards this morphology in western Mexico (Guerrero) where populations of *P. ferrugineus* come closest to those of *P. janzeni*.

Distribution and biology.—First recognized by Janzen (1967a, 1969, 1973) as a distinct but undescribed species, *P. janzeni* is confined to a limited area in western Mexico (Fig. 70) where it is sympatric with the much darker colored and com-

moner *P. veneficus*. Colonies occupy *Acacia hindsii* and are polygynous; additional details of the life history can be found in Janzen's (1973) paper on polygynous acacia-ants.

Material examined. Type material listed above, plus the following (LACM, MCZC, PSWC, UCRC, USNM).—

MEXICO *Jal.*: Puerto Vallarta (J.A.Comstock); *Nay.*: 14.5mi E San Blas (D.H.Janzen); 2mi E San Blas (R.van den Bosch); 31mi N Tepic (D.H.Janzen); 36mi N Tepic (D.H.Janzen); 4mi E San Blas (M.Irwin; M.Irwin & E.I.Schlinger; E.I.Schlinger); 5mi E San Blas (F.Parker & D.Miller); Compostela (c.u.); Rio Palillo, 14mi E San Blas (D.H.Janzen); Tepic (H.A.Scullen); *Sin.*: 20mi E Villa Union (E.I.Schlinger).

***Pseudomyrmex mixtecus* Ward, sp. nov.**

(Figs. 15, 26, 55, 61, 69)

Holotype worker.—MEXICO, Guerrero: 25.4 mi. S. Chilpancingo, 10.viii.1966, D. H. Janzen #M008810966 (LACM). HW 0.97, HL 1.07, EL 0.48, PL 0.55, PH 0.35.

Paratypes.—Same data as holotype, and three other accession numbers (M007810966, M009810966, M010810966) with same locality, date, and collector: series of 43 workers, 34 queens and 17 males (AMNH, BMNH, CASC, EBCC, GBFM, INBC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material is listed below.

Worker measurements (n=13).—HL 0.94-1.19, HW 0.89-1.03, MFC 0.054-0.073, CI 0.86-0.95, REL 0.42-0.47, REL2 0.46-0.52 OOI 1.22-2.28, VI 0.61-0.73, FCI 0.056-0.073, SI 0.43-0.45, SI2 0.86-0.97, NI 0.60-0.65, PLI 0.60-0.68, PWI 0.60-0.68, PPWI 1.40-1.73.

Worker diagnosis.—Similar to *P. ferrugineus* (q.v.) except as follows. Size smaller (HW < 1.04, LHT < 0.90), head broad (CI > 0.85); frontal carinae separated by about basal scape width or less (FCI2 0.45-0.54). Basal and declivitous faces of propodeum forming a less obtuse angle in profile than typical for *P. ferrugineus* (compare Figs. 26 and 27). Head densely punctulate, opaque. Standing pilosity rather common, usually some setae exceeding 0.12 mm and 0.20 mm in length on

mesosoma dorsum and petiole, respectively. Pubescence dense but appressed. Very dark brown to black, appendages lighter.

Comments.—*P. mixtecus* is distinguished from all other species, except *P. veneficus* and *P. flavicornis*, by its laterally rounded median clypeal lobe, broad head, and black (or very dark brown) body. It differs from *P. veneficus* by the fully opaque head, absence of conspicuous suberect pubescence on the petiole, and larger size. *P. mixtecus* is evidently closely related to *P. flavicornis* but averages smaller in size (compare worker HW and LHT values), a difference which is absolute in queens (queen HW 0.96-1.01 (n=8), whereas queen HW > 1.11 in *P. flavicornis*). In addition the petiole is relatively longer and higher, for a given head width, in both workers and queens of *P. mixtecus* (Figs. 44-47).

Distribution and biology.—*P. mixtecus* is known only from the Mexican states of Guerrero and Oaxaca (Fig. 69). Colonies have been collected from *Acacia hindsii* and *A. collinsii*, but little more has been recorded about their biology. Janzen's field notes indicate that this species is monogynous.

Material examined. Type material listed above, plus the following (CUIC, LACM, MCZC, MZSP, PSWC, SEMC, USNM, WPMC).—

MEXICO *Gro.*: 10mi NE Acapulco (D.H.Janzen); 29.6mi N Acapulco, 1400ft. (D.H.Janzen); 30mi N Acapulco, Hwy.95 (Cornell Univ. Mex. Field Party); 57.8mi S Chilpancingo, Hwy.95 (D.H.Janzen); 74km N Acapulco (W.MacKay); Acapulco (Baker; F.Knab; N.L.H.Krauss; L.J.Lipovsky); Puerto Marques (N.L.H.Krauss); San Geronimo de Juarez (W.von Hagen); *Oax.*: 11.4-17.0mi W Tehuantepec (D.H.Janzen); 13.8mi W Tehuantepec, 1500ft. (D.H.Janzen); 19km N San Pedro Pochutla, 200m (W.MacKay); 6.0mi E Niltpec, Hwy.190, 100m (D.H.Janzen).

***Pseudomyrmex nigrocinctus* (Emery 1890)**

(Figs. 13, 22, 56, 72)

***Pseudomyrma nigrocincta* Emery 1890:64.** Syntype workers, queens, males, Alajuela, Costa Rica (A. Alfaro) (BMNH, MCSN, MCZC, MHNG) [Examined]. One syntype worker from MCSN

here designated LECTOTYPE.

Pseudomyrma alfari Forel 1906:228. Two syntype workers, Tivives, embouchure de Jesus-Maria, Costa Rica (A. Alfaro) (MHNG) [Examined]. One syntype here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma nigrocincta var. *bicincta* Santschi 1922:347. Syntype workers, Costa Rica (MHNG, NHMB) [Examined]. One syntype from NHMB here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma peltata Menozzi 1927a:273. Three syntype workers, San José, Costa Rica (H. Schmidt) (NHMB) [Examined]. **Syn. nov.**

Pseudomyrmex nigrocincta [sic] (Emery); Janzen 1966:252.

Pseudomyrmex nigrocinctus (Emery); Kempf, 1972:221.

Worker measurements (n=21).—HL 0.89-1.08, HW 0.74-0.85, MFC 0.035-0.051, CI 0.75-0.84, REL 0.40-0.45, REL2 0.51-0.56, OOI 1.39-2.76, VI 0.62-0.78, FCI 0.044-0.065, SI 0.44-0.48, SI2 0.81-0.89, NI 0.58-0.64, PLI 0.59-0.68, PWI 0.49-0.61, PPWI 1.10-1.30.

Worker diagnosis.—Small species with elongate head and short eyes (REL 0.45, REL2 0.56, EL/LHT 0.61). Palp formula 5.3. Median clypeal lobe rather narrow, its surface and anterior margin convex. Frontal carinae separated by about basal scape width (FCI 0.055). Metanotal groove well marked; basal and declivitous faces of propodeum subequal (Fig. 22). Petiole short (PLI > 0.57), its anterior peduncle broad in dorsal view (PWI 0.50-0.61) and not well differentiated from the node (Fig. 22). Petiole lacking expanded posterolateral corners. Postpetiole less broad than in most other species in the *P. ferrugineus* group (see PPWI values). Head densely punctulate and subopaque, becoming sublucid posteriorly where the punctulae are separated by shiny interspaces. Mesosoma punctulate to (laterally) coriarius-imbricate, sublucid, becoming subopaque on the propodeum. Standing pilosity moderately common (as in Fig. 22); pubescence dense and closely appressed. Orange-brown, often with anterolateral fuscous patches on abdominal tergite IV (these form a distinct

transverse black band in queens).

Comments.—Workers and queens of *P. nigrocinctus* are easily distinguished from all other acacia ants, except *P. particeps* (see below), by their small size (HW < 0.86 in both castes), elongate head in the worker (worker CI < 0.85), and narrow petiole and postpetiole (worker PWI 0.50, worker PPWI 1.30, queen PWI 0.57-0.63). The orange color and short eyes are also characteristic.

Distribution and biology.—*P. nigrocinctus* is found from Guatemala to Costa Rica, with most records coming from the southern end of its range (Fig. 72). Colonies are monogynous, and have been collected from *Acacia collinsii*, *A. cornigera* and *A. hindsii*. Records from *Acacia gentilei* and *A. globulifera* (Beulig & Janzen 1969:59) need to be confirmed because of possible confusion with *P. peperii*. Janzen's (1967b) observations on "*P. nigrocincta*" in Mexico refer to *P. peperii*. On the other hand descriptions of the biology and behavior of *P. nigrocinctus* in Costa Rica (Janzen 1973, 1974, 1975, 1983; Beulig & Janzen 1969) are reliably attributed to *P. nigrocinctus*.

Material examined (AMNH, ANSP, INBC, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, PSWC, USNM, WPMC).—

COSTA RICA Alajuela: Alajuela (A. Alfaro); Atenas (A. Alfaro); Cascajal (A. Alfaro); Escobal (A. Alfaro); Ojo de Agua (A. Alfaro); Turricares (P.P. Calvert); **Guanacaste:** 1.4mi N La Cruz (D.H. Janzen); 10.7mi NW Liberia (D.H. Janzen); 10mi NW Liberia, 70m (D.H. Janzen); 10mi NW Liberia, 70m [=10.7mi NW Liberia] (D.H. Janzen); 2mi S Cañas (D.H. Janzen); 4km N Cañas (D.H. Janzen); 5km S Liberia (D.H. Janzen); 7km N Cañas (D.H. Janzen); El Coco (R.J. Hampton); Finca Taboga, 6mi S, 6mi W Cañas (D.H. Janzen); Garita (A. Alfaro); Hda. La Pacifica, nr. Cañas, 50m (P.S. Ward); La Cueva, 12km N Liberia (D.H. Janzen); Palo Verde (D.E. Gill; D.H. Janzen); Palo Verde, 50m (D.M. Olson); Santa Cruz (P.P. Calvert); Santa Rosa Natl. Pk., 290m (P.S. Ward); Santa Rosa Natl. Pk., 300m (J. Longino; P.S. Ward); Santa Rosa Natl. Pk., 5m (P.S. Ward); Santa Rosa Natl. Pk., <5m (P.S. Ward); Tempisque (A. Alfaro); **Puntarenas:** 2km E Tivives, <5m (L.S. Farley); Tivives (A. Alfaro); **San José:** 3.5km NE Santiago de Pur (D.H. Janzen); San José

(H.Schmidt; c.u.); *prov. unknown*: "Costa Rica" (c.u.).

GUATEMALA *Zacapa*: 2.0mi NE Rio Hondo, 190m [on CA-9] (D.H.Janzen); 22.3mi SW Quirigua [on CA-9] (D.H.Janzen).

HONDURAS *Choluteca*: 7.4mi NE Choluteca, 150m (D.H.Janzen).

NICARAGUA *Boaco*: 11.7mi E San Benito (D.H.Janzen); *Estelí*: 13.1mi N San Isidro (D.H.Janzen); 2.5mi N Condega, 620m (D.H.Janzen); 6.8mi N San Isidro, 780m (D.H.Janzen); 7.5mi NW San Isidro, 550m (D.H.Janzen); *León*: Izapa (J.M.Maes); *Madriz*: 3mi W Somoto, 650m (D.H.Janzen); *Matagalpa*: 15.8mi NW Sebaco (D.H.Janzen); 2.6mi N Dario (D.H.Janzen); 4.5mi SE Dario (D.H.Janzen); 4mi S Dario, 350m (D.H.Janzen); *Rivas*: 1km W Peñas Blancas (D.H.Janzen); C.R. border, 1mi N Peñas Blancas, <5m [=1mi NW Peñas Blancas] (D.H.Janzen); Isla Ometepe (F.Joyce).

Pseudomyrmex particeps Ward, *sp. nov.*

(Figs. 14, 23, 54, 57, 72)

Holotype worker.—COSTA RICA, *Puntarenas*: Rincon, Peninsula Osa, 3.iii.1965, D.H. Janzen #III (LACM). HW 0.83, HL 1.10, EL 0.50, PL 0.50, PH 0.31.

Paratypes.—Same data as holotype: series of 82 workers, 14 males, one queen (AMNH, BMNH, CASC, GBFM, INBC, JTLC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material listed below.

Worker measurements (n=12).—HL 0.93-1.10, HW 0.77-0.83, MFC 0.037-0.050, CI 0.75-0.84, REL 0.44-0.48, REL2 0.55-0.60, OOI 1.47-1.96, VI 0.65-0.75, FCI 0.048-0.062, SI 0.45-0.49, SI2 0.78-0.83, NI 0.53-0.62, PLI 0.58-0.66, PWI 0.55-0.60, PPWI 1.03-1.26.

Worker diagnosis.—Very similar to *P. nigrocinctus* (q.v.) except as follows. Eyes longer (REL2 0.55-0.60, EL/LHT 0.59-0.64) (Figs. 14, 42, 43). Front of head more strongly shining. Medium to dark brown; gaster uniformly dark brown or black; mandibles, fronto-clypeal complex, and appendages lighter brown.

Comments.—*P. particeps* is obviously a very close relative of the allopatric *P. nigrocinctus*, but

there are consistent differences between the two in eye size and color which exceed the limits of variation seen throughout the much wider range of *P. nigrocinctus*. Workers in the type series of *P. particeps* also have more elongate heads than those of *P. nigrocinctus* but this distinction is not seen in other samples. Differences between queens of the two species are more striking with the two known queens of *P. particeps* having more elongate heads (CI 0.61, compared with 0.67-0.72 in a sample of 13 *P. nigrocinctus* queens) and longer metatibiae relative to head width (LHT/HW 1.12 versus 0.97-1.07 in *P. nigrocinctus*). Additional alates of *P. particeps* are needed to confirm these differences and the apparent distinctions in male genitalia (see male key).

Distribution and biology.—*P. particeps* is a rare species known only from the Osa Peninsula and one adjacent locality, in Costa Rica (Fig. 72). It appears to be associated exclusively with *Acacia allenii*, a forest species (see Janzen, 1974 for more information about the host plant). In contrast, *P. nigrocinctus* is found farther north in more open habitats where it typically inhabits *Acacia collinsii*. The differences in worker morphology between *P. particeps* and *P. nigrocinctus* (darker color and more elongate head and/or eyes in the former) parallel those observed between populations of *P. spinicola* from the same areas (see below under *P. spinicola*), suggesting similar selection pressures associated with more forested habitats and partial (*P. spinicola*) or exclusive (*P. particeps*) occupancy of a different *Acacia* species.

Material examined. Type material listed above, plus the following (JTLC, LACM, PSWC).—

COSTA RICA *Puntarenas*: 4mi S Rincón (D.H.Janzen); Bahia Drake, Osa Penin. (F.Joyce); Corcovado Natl. Pk., Sirena, 50m (J.T.Longino); Rincón (A.R.Moldenke); *San José*: 16.7mi SW San Isidro on Hwy.22, 160m (D.H.Janzen).

*Pseudomyrmex peper*i (Forel 1913)

(Figs. 12, 24, 58, 71)

*Pseudomyrmex peper*i Forel 1913:213. Syntype workers, Patulul, Guatemala (Peper) (MHNG) [Examined]. One syntype here designated LECOTYPE.

Pseudomyrma spinicola race *convarians* Forel 1913:214. Syntype worker, Patulul, Guatemala (Peper) (MHNG) [Examined] [Synonymy by Ward 1989:452].

Pseudomyrma sabanica [sic] var. *saffordi* Enzmann 1945:89. Syntype workers, Yerba Santa, Chiapas, Mexico (G. N. Collins) (MCZC) [Examined] One syntype here designated LECTO-TYPE. [Synonymy by Ward 1989:452].

Pseudomyrmex peperi (Forel); Kempf 1972:222.

Worker measurements (n=53).—HL 0.86-1.13, HW 0.76-0.90, MFC 0.034-0.064, CI 0.76-0.89, REL 0.45-0.50, REL2 0.54-0.62, OOI 1.15-2.06, VI 0.59-0.79, FCI 0.042-0.071, SI 0.44-0.49, SI2 0.76-0.88, NI 0.62-0.71, PLI 0.54-0.65, PWI 0.63-0.75, PPWI 1.41-1.83.

Worker diagnosis.—Small species (HW < 0.92) with moderately elongate head (Fig. 12); anterior margin of median clypeal lobe straight or slightly produced medially, laterally rounded or subangulate (never sharply angulate as in *P. spinicola* and *P. satanicus*). Palp formula 4,3, rarely 5p4,3. Frontal carinae separated by about basal scape width. Mesosomal and petiolar profile typically as in Fig. 24, but in some workers basal and declivitous faces of propodeum less well differentiated and/or anteroventral tooth of petiole more prominent. Petiole and postpetiole broad, the former subtriangular in dorsal view with well developed posterolateral angles (Fig. 24). Dorsum of head obscurely punctulate-coriarius, matte. Remainder of body with finely punctulate to punctulate-coriarius sculpture, opaque to sublucid; propodeum lacking overlying rugulo-punctate sculpture seen in *P. ferrugineus*. Standing pilosity not especially abundant, sometimes lacking (worn?) on mesonotum. Appressed pubescence abundant but very fine. Light to medium brown, rarely dark brown, the gaster sometimes darker than the rest of body; appendages lighter.

Comments.—*P. peperi* is recognized by the features mentioned above and in the key. The combination of small elongate head, broad posterolaterally angulate petiole, and matte head surface is found in no other acacia ant workers or queens.

Distribution and biology.—This species has a rather wide distribution, from eastern Mexico to

Nicaragua (Fig. 71). It has been collected from *Acacia chiapensis*, *A. collinsii*, *A. cornigera*, *A. gentlei*, *A. globulifera* and *A. hindsii*. *P. peperi* is apparently polygynous over much of its range, and often occurs sympatrically with the commoner *P. ferrugineus*. Some aspects of its biology in Mexico are discussed by Janzen (1967b) under the name "*P. nigrocincta*".

Material examined (AMNH, BMNH, CASC, INHS, LACM, MCZC, MNHG, MZSP, NHMV, PSWC, SEMC, UCDC, USNM).—

BELIZE *Belize*: 16mi SW Belize, rd. to Cayo (D.H.Janzen); 5.5mi NW Belize, rd. to Chetumal (D.H.Janzen); *Cayo*: 20km S Augustine, 300m (G.D.Alpert); San Ignacio (S.E.Schoenig); *Corozal*: 15mi S Sta.Elena (Louisville) (D.H.Janzen).

EL SALVADOR *Ahuachapan*: 7.8mi S Hachadura (D.H.Janzen); *Chalatenango*: 2.5mi N Tejutla, rd. to La Palma, 580m (D.H.Janzen); 4.7mi NW La Palma, 880m (D.H.Janzen); 5.5mi SE La Palma, 1130m (D.H.Janzen); 7.5mi SE Tejutla, 320m (D.H.Janzen); *La Libertad*: 2-4km S Quezaltepeque (W.L.Brown); 2mi E La Libertad (D.H.Janzen); 5mi N Quezaltepeque (M.E.Irwin); 7.4mi N La Libertad (D.H.Janzen); Hda. Capolinas, 5km NW Quezaltepeque, 450m (M.E.Irwin); Quezaltepeque (M.E.Irwin); Santa Tecla [=Nueva San Salvador] (P.Berry); *La Unión*: 7.1mi W Amatillo, 190m (D.H.Janzen); between La Unión & San Miguel, 100m [=22.3mi S Sirama] (D.H.Janzen); between La Unión & Usulután, 150m [=2.6mi S Sirama] (D.H.Janzen); *Lapaz*: 11.6mi W Zacatecoluca, 0m (D.H.Janzen); *San Miguel*: between La Unión & San Miguel, 110m [=22.3mi E Usulután] (D.H.Janzen); *Santa Ana*: 5.3mi NW Santa Ana, 660m (on Hwy.1) (D.H.Janzen); *Sonsonate*: 24.2mi SE Hachadura (D.H.Janzen); 4.5mi S Sonsonate (D.H.Janzen); 41.4mi NW La Libertad, 10m (D.H.Janzen).

GUATEMALA *Alta Verapaz*: San Joaquín, nr. San Cristóbal Verapaz, 1080m (D.H.Janzen); *El Progreso*: 24.5mi NE Cd. Guatemala [on CA-9] (D.H.Janzen); *Escuintla*: 1.7mi S Escuintla, 370m [on CA-2] (D.H.Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H.Janzen); Escuintla (W.M.Wheeler); San José (E.S.Ross; E.I.Schlinger & E.S.Ross); *Guatemala*: 19km S Cd. Guatemala

[on CA-9] (D.H.Janzen); 20mi SE Cd. Guatemala, 1060m [on CA-1] (D.H.Janzen); 7.9mi S Cd. Guatemala, 1360m [on CA-9] (D.H.Janzen); Escuintla-Cd. Guatemala [=19km S Cd. Guatemala] (D.H.Janzen); *Izabal*: 9.9mi SW Quiriguá (D.H.Janzen); Lago Izabal, 1.5km NE El Estor (D.H.Janzen); Quiriguá (D.H.Janzen); W.M.Wheeler; nr. Mariscos (D.H.Janzen); *Jutiapa*: 11.5mi W Jutiapa, 900m (D.H.Janzen); 12.3mi E Guazacapán (D.H.Janzen); 2.3mi NW Pijiji [=Pijije] (D.H.Janzen); 23mi E Taxisco (G.F. & S.Hevel); 3.4mi N San Cristóbal, rd. to Jutiapa, 400m (D.H.Janzen); 47mi SE Escuintla, 250m [=47mi S Escuintla] (D.H.Janzen); 6.9mi N San Cristóbal, 290m (D.H.Janzen); 8.4mi N San Cristóbal, 280m (D.H.Janzen); 9.7mi E Jutiapa, 750m (hwy.to San Cristóbal) [=9.3mi NE Jutiapa] (D.H.Janzen); *Petén*: 70km NW Tikal (W.R.Tschinkel); Tikal (D.H.Janzen; W.R.Tschinkel); *Retalhuleu*: 2mi NE Champerico (D.H.Janzen); 5mi W Retalhuleu (D.H.Janzen); 5mi W Retalhuleu, Hwy.CA-2, at Rio Nil (D.H.Janzen); *Santa Rosa*: 6mi S Guazacapán (D.H.Janzen); *Suchitepéquez*: Patulul (Peper); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.0mi NE Rio Hondo, 190m [on CA-9] (D.H.Janzen); 2.6mi SW El Lobo, 100m [on CA-9] [=16.6mi NE Piedras de Afilar] (D.H.Janzen); 5.6mi NE Rio Hondo, 250m [on CA-9] (D.H.Janzen); 8.1mi SW Los Amates, 160m [on CA-9] [=8.0mi NE El Lobo] (D.H.Janzen); 9.7mi NE Piedras de Afilar, 150m [on CA-9] [=9.5mi SW El Lobo] (D.H.Janzen); Zacapa (W.M.Wheeler); km142 on Guatemala-Pto.Barrios Rd. nr. Los Amates (D.H.Janzen).

HONDURAS *Choluteca*: 19.3mi SW San Marcos de Colón, on Hwy.1 (D.H.Janzen); 19mi NE Choluteca (D.H.Janzen); 20.4mi SW San Marcos de Colón, 490m (D.H.Janzen); 3.6mi W Choluteca, 200m (D.H.Janzen); 7.4mi NE Choluteca, 150m (D.H.Janzen); *Colón*: Trujillo, 80m (Echternacht); *Comayagua*: 11.7mi S San Antonio, 830m (D.H.Janzen); 4mi N Comayagua, 500m (D.H.Janzen); *Cortés*: 24.6mi SW San Pedro Sula, 240m (D.H.Janzen); *Francisco Morazán*: 24.3mi S Camayagüela (=Tegucigalpa), 1000m (D.H.Janzen); 30.4mi S Camayagüela (D.H.Janzen); 30.5mi S Camayagüela, 930m

(D.H.Janzen); *Ocatepeque*: 2.3mi E [Nueva] Ocatepeque, 1090m (D.H.Janzen); Nueva Ocatepeque, 910m (D.H.Janzen); *Santa Bárbara*: 13.7mi SW Quimistán, 320m (D.H.Janzen); *Valle*: 18.5mi W Jicaro Galan (D.H.Janzen); 4.6mi E Jicaro Galan, 190m (D.H.Janzen).

MEXICO *Camp.*: 0.1mi S Tenabo, rd. to Becal (D.H.Janzen); 0.8mi E Campeche (D.H.Janzen); 29mi E & 12mi S Campeche (Ruinas Edzna) (D.H.Janzen); 29mi E Campeche (D.H.Janzen); 48mi NE Puerto Real (Isla Aguada, Hwy.180 (D.H.Janzen); 5mi S Tenabo (Campeche-Becal Rd.) (D.H.Janzen); Campeche (N.L.H.Krauss); *Chis.*: 2.4mi E Chiapa de Corzo, Hwy.190, 580m (D.H.Janzen); 2km N Yxhuatan [Ixhuatán], "2mi N Tapilula" (D.H.Janzen); 32mi W [San] Cristóbal de las Casas, Hwy.190 (D.H.Janzen); 3km ENE Chiapa de Corzo, 500m (P.S.Ward); 3mi N Soyalo [on Hwy.195] (D.H.Janzen); 42.5mi S Comitán, Hwy.190, 680m (D.H.Janzen); 5.4mi E Chiapa de Corzo, Hwy.190, 770m (D.H.Janzen); 56.9mi NE [NW?] Tapachula [on Hwy.200?] (D.H.Janzen); 7.0mi NE [NW?] Tapachula [on Hwy. 200?] (D.H.Janzen); 7.5mi NW Cd.Cuauhtemoc, Hwy.190 (D.H.Janzen); 8.5mi S La Trinitaria, Hwy.190 (D.H.Janzen); Finca Esmeralda (R.Nettel F.); Puerto de San Benito [=Puerto Madero] (R.Nettel F.); Tonalá, 40m (D.H.Janzen); Yerba Santa (G.N.Collins); *Hgo.*: 2km W Orizatlán, 245m (W.MacKay); *Oax.*: 11.4-17.0mi W Tehuantepec (D.H.Janzen); 19km N San Pedro Pochutla, 200m (W.MacKay); 3.9mi E Tehuantepec (D.H.Janzen); 5.7mi W "Tapanatepec" [=Tapanatepec] (D.H.Janzen); 6.0mi E Niltpec, Hwy.190, 100m (D.H.Janzen); 8.1mi W Niltpec, Hwy.190, 60m (D.H.Janzen); Temascal (D.H.Janzen); Temascal, 25m (D.H.Janzen); *Q.Roo*: 12.2mi S Peto, Q.Roo-Yucatan border (D.H.Janzen); 26.6mi S Felipe Carrillo Puerto (D.H.Janzen); 5.4mi E Polyuc (D.H.Janzen); Cancun (A.Dejean); Cenote de Las Ruinas, 8km NW Polyuc (J.Red et al.); Chetumal (J.C. & D.Pallister); San Miguel, Cozumel I. (N.L.H.Krauss); Sian Ka'an (A.Dejean); Sian Ka'an Reserve, nr. Felipe Carrillo Puerto (A.Dejean); *S.L.P.*: 2mi N Rio Amahac, Tamazunchale, 400ft. (W.S.Creighton); 6mi NW Tamazunchale, 600ft. (Univ.Kansas Mex.Exped.); 8mi W San Joachin (W.J.Gertsch); El Bonito, 7mi S Cd. Valles,

300ft. (P.H. & M.Arnaud); El Salto (W.E.LaBerge); Tamazunchale (D.H.Janzen); Tamazunchale, 600ft. (W.S.Creighton); *Ver.*: 29.5mi NW Tuxpan, Hwy.122 [actually Hwy.127] (D.H.Janzen); Alazan (F.Parker & D.Miller); Cordoba (W.M.Mann); Cotaxtla Exp. Sta., Cotaxtla (D.H.Janzen); Mirador (E.Skwarra); Veracruz (E.Skwarra); *Yuc.*: 30mi S Merida (P.J.Spangler); 8mi E Merida (rd. to Pto. Juarez) (D.H.Janzen); Itzimna (J.C. & D.Pallister); Merida (D.H.Janzen; N.L.H.Krauss); Oxtutzcab (D.H.Janzen); Sta. Elena, S of Ticul, "Hwy.180" [prob.Hwy.261] (D.H.Janzen); *state unknown*: "Mex" ("Norton").

NICARAGUA *Esteli*: 1mi N Condega, 500m (D.H.Janzen); 2.5mi N Condega, 620m (D.H.Janzen); *León*: San Jacinto (J.M.Maes); *Madriz*: 3mi W Somoto, 650m [=2.5mi W Somoto] (D.H.Janzen); *Nueva Segovia*: 7.1mi W Amatillo (D.H.Janzen).

Pseudomyrmex satanicus (Wheeler 1942)
(Figs. 10, 20, 59, 68)

Pseudomyrma satanica Wheeler 1942:174. Syntype workers, queen, male, Rio Agua Salud, Canal Zone, Panama (W. M. Wheeler) (AMNH, LACM, MCZC) [Examined]. One MCZC syntype worker here designated LECTOTYPE. *Pseudomyrmex satanica* [sic] (Wheeler); Janzen 1966:252.

Pseudomyrmex satanicus (Wheeler); Kempf 1972:223.

Worker measurements (n=15).—HL 1.16-1.36, HW 1.10-1.26, MFC 0.035-0.057, CI 0.90-0.97, REL 0.45-0.50, REL2 0.48-0.52, OOI 0.92-1.67, VI 0.69-0.78, FCI 0.030-0.049, SI 0.45-0.49, SI2 0.88-1.00, NI 0.63-0.68, PL1 0.47-0.54, PW1 0.46-0.63, PPW1 1.35-1.54.

Worker diagnosis.—Similar to *P. spinicola* (q.v.) except as follows. Larger (HW > 1.09), head broader (CI > 0.88) (Fig. 34) with straight or slightly concave posterior margin and subangulate posterolateral corners (Fig. 10). (The posterior margin of the head approaches this condition in some *P. spinicola* workers but these have much smaller, more elongate heads, HW < 1.10, CI < 0.90.) Median clypeal lobe narrower (CLW/HW 0.20-0.22; see Fig. 33).

Palp formula 4,3. Head with pronounced pit-like impression below the median ocellus (absent or poorly developed in *P. spinicola*). Metanotal groove better developed, longer. Petiole tending to be more slender, with less distinct posterolateral corners (this characteristic seen in some workers of *P. spinicola*, especially individuals from Panama). Body pubescence averaging thicker than in *P. spinicola*. Dark brown in color, mandibles and appendages lighter.

Comments.—The foregoing diagnosis will allow discrimination of *P. satanicus* workers from those of the closely related *P. spinicola*; queens can be recognized by size alone (HL > 1.65, HW > 1.20). *P. satanicus* can be distinguished from the remaining members of the *P. ferrugineus* group by the emarginate, laterally angulate median clypeal lobe of the worker and the large size of the queen.

Distribution and biology.—*P. satanicus* is a forest species restricted to a few localities in central Panama where its host plant, *Acacia melanoceras*, grows (Fig. 68). Both the ant and plant are intolerant of forest clearance and are considered vulnerable to extinction (Janzen 1974). The ant is polygynous, with 5-20 or more queens per colony, and the workers are particularly aggressive, even for acacia-ants (Wheeler 1942; Janzen 1974). See Janzen (1974:43-53) for additional details on *P. satanicus* and its host plant.

Material examined (AMNH, LACM, MCZC, PSWC, USNM).—

PANAMA *Canal Zone*: "Canal Zone" (A.H.Jennings); 3mi SW Gatún Dam (D.H.Janzen); Barro Colorado Island (D.H.Janzen); France Field (G.C.Wheeler); Marajal [Majagual] nr. Colon (W.M.Wheeler); Red Tank (W.M.Wheeler); Rio Agua Salud (W.M.Wheeler); Zorra Island (D.H.Janzen); *Panamá*: Rio Piedras (D.H.Janzen); *prov. unknown*: "Panama" (c.u.).

Pseudomyrmex spinicola (Emery 1890)
(Figs. 11, 21, 60, 68)

Pseudomyrma spinicola Emery 1890:64. Lectotype worker. Alajuela, Costa Rica (Alfaro) (MCSN) [Examined].

Pseudomyrma spinicola race *atrox* Forel 1912:24.

Syntype workers, Panama (Christophersen) (MHNG, NHMB) [Examined]. **Syn. nov.** One syntype from MHNG here designated LECTOTYPE.

Pseudomyrma spinicola race *Gaigei* Forel 1914:615. Syntype workers, Columbian (Gaige) (MHNG), Fundacion, Colombia (F. M. Gaige) (LACM, MCZC) [Examined]. **Syn. nov.**

Pseudomyrma spinicola subsp. *infernalis* Wheeler 1942:180. Syntype workers, queens, males, Venado, Canal Zone, Panama (W. M. Wheeler), Red Tank, Canal Zone, Panama (W. M. Wheeler), and Las Sabanas, Panama (W. M. Wheeler) (AMNH, MCZC) [Examined]. One MCZC worker, from Red Tank, here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma spinicola subsp. *scelerosa* Wheeler 1942:181. Syntype workers, Granada, Nicaragua (C. F. Baker) (AMNH, MCZC) [Examined]. One MCZC worker here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma spinolae [sic] var. *infernalis* Enzmann 1945:91. Syntype workers, queens, Red Tank, Canal Zone, Panama (W. M. Wheeler) (MCZC) [Examined] [Objective synonym of *P. spinicola* subsp. *infernalis* Wheeler; Brown 1949:43].

Pseudomyrma spinolae [sic] var. *scelerosa* Enzmann 1945:91. Syntype workers, Granada, Nicaragua (C. F. Baker) (MCZC) [Examined] [Objective synonym of *P. spinicola* subsp. *scelerosa*, Wheeler; Brown 1949:43].

Pseudomyrmex spinicola (Emery); Wheeler and Wheeler 1956:386.

Worker measurements (n=41).—HL 0.99-1.28, HW 0.94-1.15, MFC 0.032-0.067, CI 0.84-0.97, REL 0.42-0.47, REL2 0.45-0.54, OOI 1.22-2.77, VI 0.64-0.83, FCI 0.032-0.061, SI 0.45-0.50, SI2 0.88-1.05, NI 0.61-0.69, PLI 0.47-0.64, PWI 0.49-0.71, PPW1 1.32-1.85.

Worker diagnosis.—Median clypeal lobe emarginate, laterally angulate (Fig. 11), relatively broad (CLW/HW 0.21-0.25). Palp formula 5,3 (rarely 5p4,3). Frontal carinae relatively close, and median lobes of antennal sclerites rather exposed (FCI2 0.24-0.42). Head longer than broad but variably so (see range of CI values). Posterior

margin of head ranging from broadly convex (Fig. 11) to straight or even weakly concave, usually rounding gently into the sides of head. Basal face of propodeum subequal to declivitous face, rounding into latter; in dorsal view propodeal spiracles salient, protruding laterally. Petiole generally slender (PLI <0.65) with a well developed anterior peduncle; in dorsal view posterolateral angles typically prominent. Head densely punctulate, sublucid, interspaces small (punctulae essentially contiguous on most of head) but shiny. Mesosoma finely punctulate dorsally becoming punctulate-coriaceous laterally, sublucid; propodeum lacking overlying, coarser rugulo-punctate sculpture. Standing pilosity usually moderately common on body dorsum and including some hairs > 0.20 mm. Appressed pubescence common on most surfaces. Varying from light orange-brown to dark brown in color.

Comments.—The short, broad, emarginate and laterally angulate median clypeal lobe (Fig. 11) distinguishes the worker of this species. The sublucid integument, elongate petiole, prominent propodeal spiracles, and somewhat angulate posterolateral corners of the petiole are also characteristic. In addition, queens and workers of *P. spinicola* have more elongate scapes and legs than those of all other species except *P. satanicus* (Figs. 30, 31). For differences between *P. spinicola* and the closely related *P. satanicus* see under the latter species.

P. spinicola is a variable taxon and has received several infraspecific names, here considered junior synonyms. Southeastern populations (from the Río Grande de Tárcoles in Costa Rica east through Panama to northern Colombia) are somewhat differentiated from the others, with the workers and queens tending to have more elongate heads, darker color, and more slender petioles with less pronounced posterolateral angles (see Figs. 34, 35). In Costa Rica the contrasts between the two sets of populations are rather striking, and are perhaps accentuated by habitat differences since some (but not all) the southeastern populations are associated with *Acacia allenii* growing in forested situations, while the northern populations are primarily from *Acacia collinsii* in open habitats. Samples from Panama (all associated with *A. collinsii*) are more variable and partly bridge the phenotypic gap. It is possible that more than one species is masquerad-

ing in this variation but the evidence remains ambiguous.

Distribution and biology.—*P. spinicola* is a monogynous species, distributed from Honduras to northern Colombia (Fig. 68), which is associated with *Acacia collinsii* and, less frequently, *Acacia allenii* and *A. cornigera*. Janzen (1983) provides a good summary of its biology in Costa Rica, under the name "*P. ferruginea*". Observations on "*P. ferruginea*" in Costa Rica, Nicaragua, Panama and Isla Providencia (Janzen 1969, 1974, 1975, 1983) refer to *P. spinicola*; true *P. ferrugineus* does not occur south of Honduras and El Salvador.

Material examined (AMNH, ANSP, BMNH, CUIC, FFIC, GBFM, GCWC, INBC, JTLC, KSUC, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, PSWC, UCDC, USNM).—

COLOMBIA *Atlántico*: Cuatro Bocas, 200m (J.F.G. Clarke); *Bolívar*: Hda. Monterey, 50m (G.Fagua; F.Fernández); *Magdalena*: Aracataca (P.J. Darlington); *Fundación* (F.M. Gaige); *Fundación, Santa Marta Mts.*, 300ft. (F.M. Gaige); *San Andrés y Providencia*: "Old Providence Isl." (D. Fairchild); *Isla Providencia*, 300ft. (D.H. Janzen); *dept. unknown*: "Columbien" (Gaige).

COSTA RICA *Alajuela*: Alajuela (A. Alfaro); *San Mateo* (P. Biolley); *Surubres*, nr. *San Mateo* (P. Biolley); *Turrúcarre* (A. Alfaro); *Cartago*: Turrialba (c.u.); *Guanacaste*: 10.7mi NW Liberia (D.H. Janzen); 2mi S Cañas (D.H. Janzen); 5km S Liberia (D.H. Janzen); 6mi W Liberia (D.H. Janzen); 7km N Cañas (D.H. Janzen); Cañas, "La Pacifica" (R.L. Jeanne); *Finca La Pacifica* (D.W. Davidson); *Garita* (A. Alfaro); *Hda. Comelco*, 24km NW Cañas (InterAm Hwy.) (E.R. Heithaus); *Hda. La Pacifica*, nr. *Cañas*, 50m (P.S. Ward); *Palo Verde* (D.E. Gill; E. Guerrant & P. Fiedler; H.A. Hespenheide; D.H. Janzen); *Palo Verde*, 50m (D.M. Olson); *Palo Verde*, <100m (J. Longino); *Rio Corobici*, nr. *Cañas* (R.M. Bohart); *Santa Rosa Natl. Pk.* (E.M. Barrows); *Santa Rosa Natl. Pk.*, 300m (J. Longino; P.S. Ward); *Santa Rosa Natl. Pk.*, 5m (P.S. Ward); *Santa Rosa Natl. Pk.*, <5m (P.S. Ward); *Heredia*: "15mi SE Pto. Viejo" [15km SW Pto. Viejo] (D.H. Janzen); *Puntarenas*: 1-5mi NW Rincón (D.H. Janzen); 14.1mi N Golfito (D.H. Janzen); 14km E Palmar Norte, 70m (P.S. Ward); 1km NE Tárcoles, 20m (P.S. Ward); 21.6 rd.mi NE Palmar Norte, 90m

(D.H. Janzen); 3.4mi SE Golfito, 30m (D.H. Janzen); 4mi SW Rincón (D.H. Janzen); *Corcovado Natl. Pk.* (D.W. Davidson; J.T. Longino); *Corcovado Natl. Pk.*, Llorona (J.T. Longino); *Corcovado Natl. Pk.*, Sirena, 100m (P.S. Ward); *Corcovado Natl. Pk.*, Sirena, 10m (P.S. Ward); *Entrada Boruca*, 20km NE Palmar Sur (D.H. Janzen); *Osa Penin.*, nr. *Rincón* (D.H. Janzen); *Reserva Biol. Carara*, 30m (P.S. Ward); *Rincón* (D.H. Janzen); *Rio Terraba*, nr. *Palmar Sur* (D.H. Janzen); *San José*: 16.4mi SW San Isidro, 160m (D.H. Janzen); 3.5km NE Santiago de Pur (D.H. Janzen); *Santa Ana* (D.H. Janzen); *Tarrazu* [Rio?] (A. Alfaro); *Villa Colón* (A. Alfaro; D.H. Janzen); *Villa Colón*, 880m (A. Alfaro).

HONDURAS *Choluteca*: 11.1mi NE Choluteca, 450m (D.H. Janzen); 3.6mi W Choluteca, 200m (D.H. Janzen); *Colón*: El Canal, Puerto Castilla (W.M. Mann); *Roatan Isl.* [Isla de Roatán] (M. Bates); *Trujillo*, 80m (Echternacht).

NICARAGUA *Boaco*: Empalme do Boaco [=El Empalme?] (Echternacht); *Chontales*: no specific locality (Janzen); *Esteli*: 7.5mi NW San Isidro, 550m (D.H. Janzen); *Granada*: Granada (C.F. Baker); *León*: 19mi SE León [=3.5mi N Pto. Somoza (Sandino)] (D.H. Janzen); 28.1mi SE León (D.H. Janzen); *Madriz*: 13.9mi from Honduras, on Nic. border, Hwy. 1 (D.H. Janzen); 2.5mi W Somoto (D.H. Janzen); *Managua*: 20mi N Tipitapa, 90m [=19.4mi N Tipitapa] (D.H. Janzen); 8.1mi E San Benito (D.H. Janzen); 9mi N Tipitapa, 50m [=8.8mi N Tipitapa] (D.H. Janzen); *Matagalpa*: 15.8mi NW Sebaco (D.H. Janzen); 2.6mi N Dario (D.H. Janzen); 4.1mi S Matagalpa, 650m (D.H. Janzen); 4mi S Dario, 350m [=4.5mi SE Dario] (D.H. Janzen); 4mi S Dario, 350m (D.H. Janzen); *Rivas*: C.R. border, 1mi N Peñas Blancas, <5m [=1mi NW Peñas Blancas] (D.H. Janzen); *Isla Ometepe* (F. Joyce); *San Juan del Sur*, 10m [=1mi N San Juan del Sur] (D.H. Janzen).

PANAMA *Canal Zone*: 7.5mi NW Balboa (between Summit Gdn. & Paraiso) (D.H. Janzen); Ancon (S.F. Blake); Barro Colorado Island (Weber); Cerro Galera (P.S. Ward); Chivachiva trail (W.M. Wheeler); Chivachiva trail, nr. Red Tank (W.M. Wheeler); Culebra [presumably Culebra Cut] (D.D. Gaillard); E end of Madden Dam (D.H. Janzen); Gamboa (N. Banks); Howard AFB,

W of Panama City, 50m (W.L.Brown et al.); Madden Dam (D.Quintero et al.); Paraiso (A.Busck); Red Tank (W.M.Wheeler); Ruta 1, 14km W Panama City, 100m (W.L.Brown et al.); Venado (W.M.Wheeler); W end Madden Dam (D.H.Janzen); *Chiriquí*: 10.7mi ESE Concepción (D.H.Janzen); 12.9mi E Remedios (D.H.Janzen); 19.6mi E Sapotilla, 50m (D.H.Janzen); 7.2mi W Remedios (D.H.Janzen); 9.5mi S Boquete, 620m (D.H.Janzen); *Coclé*: 0.3mi W Agua Dulce, 50m (D.H.Janzen); 10.4mi NE Santa Maria, 60m [=1.9mi W Agua Dulce, Hwy. 1] (D.H.Janzen); 2.7mi SW Penonome (D.H.Janzen); *Herrera*: Cerro Guacamaya, Albina al N. de Monagrillo (D.Quintero et al.); *Los Santos*: 3.1mi N Pedasi (D.H.Janzen); Azuero Penin., 5.4mi SE Los Santos, <5m (D.H.Janzen); *Panamá*: 18.6mi SW Chepo (D.H.Janzen); Bella Vista (N.Banks); Las Sabanas (G.C.Wheeler; W.M.Wheeler); Las Sabanas, Panama City (H.F.Dietz); Rio Corona, S of El Valle, 2000ft. (C.W.Rettenmeyer); Rio Tetita, San Carlos (F.D.Rattinibane); savannah nr. Juan Diaz (Weber); *Veraguas*(?): Las Palmas (c.u.); *Veraguas*: 4km NW Santiago (D.Quintero); *prov. unknown*: "Panama" (Christophersen).

Pseudomyrmex veneficus (Wheeler 1942)
(Figs. 17, 28, 62, 69)

Pseudomyrma belti subsp. *venefica* Wheeler 1942:162. Syntype workers, males, queens, Escuinapa, Sinaloa, Mexico (J. H. Batty) (AMNH, MCZC) [Examined]. One MCZC syntype worker here designed LECTOTYPE.

Pseudomyrma belti subsp. *venefica* Enzmann 1945:81. Syntype workers, queens, Manzanillo, Colima, Mexico (C. H. T. Townsend) (MCZC) [Examined] [Synonymy by Brown 1949:42].

Pseudomyrmex venefica [sic] (Wheeler); Janzen 1969:241.

Pseudomyrmex belti veneficus (Wheeler); Kempf 1972:216.

Pseudomyrmex veneficus (Wheeler); Ward 1989:439.

Worker measurements (n=12).—HL 0.95-1.04, HW 0.85-0.95, MFC 0.045-0.073, CI 0.88-0.95, REL 0.44-0.47, REL2 0.47-0.52, OOI 1.26-2.30,

VI 0.66-0.75, FCI 0.051-0.081, SI 0.43-0.46, SI2 0.85-0.94, NI 0.58-0.65, PLI 0.60-0.67, PWI 0.58-0.67, PPWI 1.35-1.73.

Worker diagnosis.—Similar to *P. ferrugineus* (q.v.) except as follows. Smaller (LHT 0.69-0.80), with broad head (CI > 0.87); frontal carinae separated by basal scape width or less (FCI2 0.40-0.60); petiole short (PL 0.43-0.54) and relatively narrow (see PWI values) with somewhat rounded posterolateral angles (Fig. 28). Head densely punctulate, subopaque to sublucid, with weak silvery reflectance. Overlying rugulo-punctate sculpture on propodeum weak and ill-defined. Standing pilosity variable in abundance, becoming rather short (0.10 mm) and sparse in southern populations. Pubescence thick and conspicuous, suberect on some surfaces especially the propodeum and petiole; suberect pubescence on petiolar dorsum contrasting with the appressed pubescence on the postpetiole (Fig. 28). Very dark greyish-brown to black, parts of the mesosoma and petiole sometimes with lighter yellowish brown (more consistently so in the queen).

Comments.—The small size (worker HW < 0.96; queen HW 0.84-0.96, n=12), conspicuous suberect pubescence on the propodeum and petiole, and black coloration of the head and gaster distinguish workers and queens of *P. veneficus*. The related species, *P. flavicornis*, is larger (worker HW > 0.98, queen HW 1.12-1.19) with a broader and more robust petiole (Figs. 25, 28). Workers and queens of *P. flavicornis* also lack the sublucid head and conspicuous suberect pubescence characteristic of *P. veneficus*. *P. mixtecus* is somewhat intermediate between these two - it has the head sculpture and pubescence typical of *P. flavicornis* but approaches *P. veneficus* in size (worker and queen head widths overlapping, although only slighter in the queens where HW 0.96-1.01 (n=8) in *P. mixtecus*) and petiolar dimensions (Figs. 44-47).

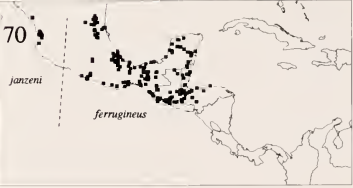
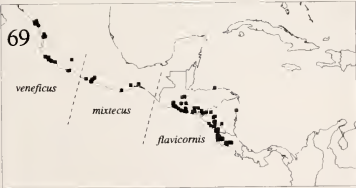
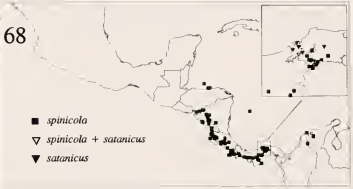
Distribution and biology.—*P. veneficus* has a limited distribution in western Mexico (Sinaloa to Michoacan) (Fig. 69) where colonies occupy *Acacia hindsii* and, at one locality, *A. collinsii*. Janzen (1973) gives a detailed description of the ecology and behavior of this highly polygynous, effectively unicolonial, species whose colonies are among the largest of all social insects (containing millions of workers and several hundred thousand queens).

Material examined (AMNH, CASC, EBCC, INHS, LACM, MCSN, MCZC, MZSP, PSWC, UCDC, UCRC, USNM).—

MEXICO *Col.*: 9.4mi NW Manzanillo (D.H.Janzen); Manzanillo (C.H.T.Townsend; W.M.Wheeler); Paso del Rio, 200ft. (I.J.Cantrall); *Jal.*: 2km E Chamela, 20m (P.S.Ward); 5km E Chamela, 50m (P.S.Ward); 6mi NE El Rincon, 1600ft. (R.J.Hamton); Barra de Navidad (N.L.H.Krauss); Chamela (R.J.McGinley; J.F.Watkins); *Mich.*: 1.1mi N Gabriel Zamora, 820m (D.H.Janzen); 1.5mi N La Mira (D.H.Janzen); 15km WNW Playa Azul, 50m (P.S.Ward); *Nay.*: 12mi

NE San Blas (W.J.Gertsch & W.Ivie); 16mi NW Tepic (W.E.LaBerge); 31mi N Tepic (D.H.Janzen); 37mi N Tepic (D.H.Janzen); 4mi E San Blas (M.E.Irwin); Rio Palillo, 14mi E San Blas (D.H.Janzen); *Sin.*: 14.6mi S Mazatlan (D.H.Janzen); 20mi E Villa Union (E.I.Schlinger); 20mi E Villa Union, 235m (M.E.Irwin; E.Schlinger et al.); 20mi S Villa Union (E.I.Schlinger); 5mi E Concordia (W.J.Gertsch & J.A.Woods); Escuinapa (J.H.Batty); Palmito (L.de Mauzo); Piedra Blanca (R.M.Bohart); *state unknown*: "Mexico"(c.u.).

OTHER ACACIA-ASSOCIATED



Figs. 67- 72. Distributions of species in the *Pseudomyrmex ferrugineus* group.

PSEUDOMYRMEX
FROM CENTRAL AMERICA

Introduction

Three of the species discussed below (*Pseudomyrmex nigropilosus*, *P. simulans* and *P. subtilissimus*) are obligate inhabitants of Central American swollen-thorn acacias, although they are not closely related to the *P. ferrugineus* group (Ward 1991). A fourth species, *P. reconditus*, is known only from a single collection, made in association with *Acacia collinsii*. The remaining six species (*P. boopis*, *P. gracilis*, *P. hesperius*, *P. ita*, *P. kuenckeli* and *P. opaciceps*) are non-specialist *Pseudomyrmex* which have been collected only occasionally from acacias. These taxa are included for completeness, and their presentation here necessitates a certain amount of taxonomic house-keeping.

One could expect additional generalist *Pseudomyrmex* to be found in living or dead acacia thorns. Menozzi (1927b) mentions collections by H. Schmidt of "*Pseudomyrma flavidula*" and "*P. brunnea*" from *Acacia "spadicigera"* (probably *A. collinsii*) near San José, Costa Rica. I have not examined the ant specimens in question but they probably belong to *P. pallidus* (F. Smith) and *P. ejectus* (F. Smith), respectively. Diagnoses of these species appear in Ward (1985). Finally, mention should be made of other Neotropical acacias which are apparently not myrmecophytes, but which may harbor opportunistic *Pseudomyrmex* species in their spines: *Acacia daemon* in Cuba with *P. pazosi*, *P. simplex* and *P. cubensis* (Berazaín & Rodríguez 1983; *Pseudomyrmex* nomenclature follows Ward 1989), and *A. caven* in Paraguay with *P. gracilis* (s.l.) and one or more species in the *P. pallidus* group (Wheeler 1942; Ward 1991).

Synonymic list of species

- P. boopis* (Roger 1863b)
 = *P. modestus* (F. Smith 1862) (preoccupied)
 = *P. thoracicus* (Norton 1868b) **syn. nov.**
 = *P. excavatus* (Mayr 1870) (Kempf 1967)
 = *P. flaviventris* (Emery 1896) (Kempf 1960)
 = *P. fusciceps* (Santschi 1931) (Kempf 1960)

= *P. guatemalensis* (Enzmann 1945) (Kempf 1960)

- P. gracilis* (Fabricius 1804)
 = *P. bicolor* (Guérin 1844) **syn. nov.**
 = *P. sericatus* (F. Smith 1855) **syn. nov.**
 = *P. dimidiatus* (Roger 1863a) **syn. nov.**
 = *P. mexicanus* (Roger 1863a) **syn. nov.**
 = *P. variabilis* (F. Smith 1877) (Ward 1989)
 = *P. pilosulus* (F. Smith 1877) **syn. nov.**
 = *P. volatilis* (F. Smith 1877) **syn. nov.**
 = *P. canescens* (F. Smith 1877) **syn. nov.**
 = *P. guayaquilensis* (Forel 1907) (unavailable name)
 = *P. glabriventris* (Santschi 1922) **syn. nov.**
 = *P. veliferus* (Stütz 1933) **syn. nov.**
 = *P. longinodus* (Enzmann 1945) (Brown 1949)
P. hesperius, **sp. nov.**
P. ita (Forel 1906) **stat. nov.**
 = *P. acaciaron* (Wheeler 1942) **syn. nov.**
 = *P. acaciaron* (Enzmann 1945) (Brown 1949)
P. kuenckeli (Emery 1890)
 = *P. dichrous* (Forel 1904) (Kempf 1961)
 = *P. bierigi* (Santschi 1932) (Kempf 1961)
 = *P. crenulatus* (Enzmann 1945) (Kempf 1961)
P. nigropilosus (Emery 1890)
P. opaciceps, **sp. nov.**
P. reconditus, **sp. nov.**
P. simulans Kempf 1958
P. subtilissimus (Emery 1890)

SPECIES ACCOUNTS

Pseudomyrmex boopis (Roger 1863b)
(Fig. 1)

Pseudomyrma modesta F. Smith 1862:32. Holotype (unique syntype) worker, Panama (Stretch) (BMNH) [Examined]. [Preoccupied by *P. modesta* F. Smith 1860 = *Tetraponera modesta* (F. Smith).]

Pseudomyrma boopis Roger 1863b:25. Replacement name for *Pseudomyrma modesta*.

Pseudomyrma thoracica Norton 1868b:8. Syntype workers, Cordova, Mexico (Sumichrast) [Not examined; see comments below]. **syn. nov.**

Pseudomyrma excavata Mayr 1870:410. Syntype workers, "N. Granada" (BMNH, MHNG, NHMV) [Examined] [Synonymy by Kempf

1967:2].

Pseudomyrma excavata var. *flaviventris* Emery 1896:2. Syntype workers, Darien, Panama (Festa) (MCSN, MHNG) [Examined] [Synonymy by Kempf 1960:22].

Pseudomyrma excavata var. *fusciceps* Santschi 1931:271. Two syntype workers, France Field, Panama (A. Bierig) (NHMB) [Examined] [Synonymy by Kempf 1960:22].

Pseudomyrma spinicola subsp. *modesta* F. Smith; Wheeler 1942:105.

Pseudomyrma tenuis var. *guatemalensis* Enzmann 1945:92. Holotype worker, Escuintla, Guatemala [Not examined] [Synonymy by Kempf 1960:22].

Pseudomyrmex boopis (Roger); Kempf 1967:2.

Worker diagnosis.—Medium-sized species (HW 1.16–1.29) in the *P. tenuis* group, with a broad head (CI 0.92–1.02), tectiform and laterally rounded median clypeal lobe, large eyes (REL 0.66), and laterally marginate pronotum. Mesosoma arched and angular in profile; petiole short, high and thin, laterally marginate, with a gently ascending anterodorsal face which rounds into a much steeper (almost vertical) posterior face (Fig. 1). Standing pilosity sparse, lacking on the mesonotum, propodeum, and petiole. Color highly variable, ranging from light testaceous brown to bicolored orange and black (usually with the gaster and pronotum lightest in color) to dark brown.

Taxonomic comments.—For a more detailed description of this species see Kempf (1960:23). I have synonymized *P. thoracicus* (Norton) under *P. boopis* on the basis of Norton's (1868b) original description and the biological notes of Sumichrast in Norton (1868a). In combination these clearly suggest *P. boopis* rather than any other *Pseudomyrmex* known to occur in southern Mexico. Although the type material of *P. thoracicus* is presumably lost, additional indirect evidence of its identity can be found in Gustav Mayr's collection in Vienna (NHMV) where there is a *P. boopis* worker from Colombia ("Neugranada") identified by Mayr as "*P. thoracica* Norton". This take son added significance when it is realized that Mayr was apparently the recipient of some of Norton's material. During a brief visit to NHMV I noted

specimens of several species, including *P. ferrugineus*, *P. peperi*, *P. elongatulus* (Dalla Torre) and *P. brunneus* (F. Smith) (although unfortunately not *P. boopis*), labelled "Mex. Norton" or "N.Am./Norton".

Distribution and biology.—*P. boopis* occurs in rainforest and tropical moist forest from southern Mexico to Ecuador, Venezuela and northern Brazil. This species is less arboreal than most *Pseudomyrmex*, and nests typically in rotten wood on or near the ground. The type specimen of *P. boopis* came from a nest in a swollen-thorn acacia (Smith 1862:33), however, and Janzen found colonies in thorns of *Acacia melanoceras* seedlings in Panama.

Pseudomyrmex gracilis (Fabricius 1804)

(Fig. 6)

Formica gracilis Fabricius 1804:405. Lectotype worker, Essequibo, Guyana (ZMUC) [Examined].

Pseudomyrma bicolor Guérin 1844:427. Syntype queen (unique?), Colombia (ZSMC) [Examined] **Syn. nov.**

Pseudomyrma sciricata F. Smith 1855:159. Holotype (unique syntype) worker, Brazil (BMNH) [Examined] **Syn. nov.**

Pseudomyrma dimidiata Roger 1863a:177. Syntype workers, Colombia (not in MNHN or ZMHB) [Not examined] **Syn. nov.**

Pseudomyrma mexicana Roger 1863a:178. Syntype workers, Mexico (not in MNHN or ZMHB) [Not examined] **Syn. nov.**

Pseudomyrma variabilis F. Smith 1877:62. Lectotype worker, Barbadoes (BMNH) [Examined] [Synonymy by Ward 1989:439].

Pseudomyrma pilosula F. Smith 1877:62. Two syntype workers, Barbadoes (BMNH) [Examined]. One syntype here designated LECTO-TYPE. **Syn. nov.**

Pseudomyrma volatilis F. Smith 1877:65. Holotype (unique syntype) male, Mexico (BMNH) [Examined] **Syn. nov.**

Pseudomyrma canescens F. Smith 1877:66. Holotype (unique syntype) queen, Abydos, Brazil (BMNH) [Examined] **Syn. nov.**

Pseudomyrma gracilis var. *glabriventris* Santschi 1922:345. Syntype workers, Izozo, Bolivia (Lizer & Delétang) (NHMB) [Examined] **Syn. nov.**

Pseudomyrma gracilis mexicana var. *guayaquilensis* Forel 1907:7. Worker, Guayaquil, Ecuador (Buchwald) (MHNG) [Examined] Unavailable infrasubspecific name.

Pseudomyrma gracilis var. *velifera* Stütz 1933:68. Holotype queen, Champerico, Guatemala (Paessler) (not in ZMUH; Weidner 1972) [Not examined] **Syn. nov.**

Pseudomyrma gracilis var. *longinoda* Enzmann 1945:87. Syntype worker, Peru (MCZC) [Examined] [Synonymy by Brown 1949:43].

Pseudomyrmex gracilis (Fabricius); Kusnezov 1953:214.

Worker diagnosis.—With the traits of the *gracilis* group (see couplet 6 of the key; p. 130) and the following more specific features. Head broad, about as wide as long (CI 0.95–1.08); anterior margin of median clypeal lobe straight to broadly convex, rounded laterally; pronotum dorsolaterally marginate but not sharply so; in lateral view mesonotum more steeply inclined than basal face of propodeum; petiole long and slender (PLI 0.46–0.57) with a distinct anterior peduncle (Figs. 6, 53); head densely punctulate with a subopaque to sublucid (not matte) appearance; standing pilosity abundant, fine, predominantly pale silvery-white (not black).

Size and color extremely variable (HW 1.39–2.07), varying from unicolorous black (appendages lighter) to unicolorous orange-brown, with many intermediate and bicolored combinations. In populations from Mesoamerica the gaster is typically black, or if paler (orange-brown) then it is usually accompanied by a similar light coloration of the mesosoma (and sometimes also the head).

Taxonomic comments.—The *P. gracilis* complex presents one of the more taxonomically challenging problems in the genus *Pseudomyrmex* and the above treatment is by no means a final solution. The worker- and queen-based forms, newly synonymized under *P. gracilis*, fall within the bounds of the preceding diagnosis, but it is quite possible that my concept of this species will prove to be too broad. The types of *P. dimidiatus*, *P. mexicanus* and *P. veliferus* could not be located. They are judged to

be junior synonyms on the basis of the original descriptions. The unique male holotype of *P. volatilis* is clearly a member of the *P. gracilis* group based on size (HW 1.48), mandibular dentition, pilosity, petiole shape, and shape of the parameres. In comparison with males of *gracilis* group species known to occur in Mexico, namely *P. gracilis*, *P. major* (see below), *P. nigropilosus* and *P. opaciceps*, the type specimen agrees best with *P. gracilis*.

The concept of *P. gracilis* adopted above encompasses an impressive amount of phenotypic variability. Collections from single regions often give the impression that this variation is distributed bimodally or multimodally, as more or less discrete morphs. For example, nest samples from Costa Rica can be segregated on the basis of worker morphology into (i) a large (HW > 1.80), usually lighter-colored form (with orange mesosoma, petiole, and postpetiole, and black head and gaster), (ii) a smaller, bicolored, usually more heavily infuscated form, and (iii) an all-black form of variable size. The first two are typically found in open or xeric habitats while the third is more common in closed forest, suggesting some ecotypic differentiation. Yet when large enough sample sizes are obtained all degrees of intermediacy in size and color are encountered, and the variation in color (less so size) can be seen among individuals (workers and alate queens) from the same nest. Thus, if there are ecotypes they do not appear to be reproductively isolated.

Left unresolved after the establishment of the above synonymy is the relationship of *P. gracilis* to the following nominal taxa: *P. alternans* (Santschi), *P. gracilis atrinodus* (Santschi), *P. gracilis argentinus* (Santschi) and *P. santschii* (Enzmann). But the following deserves recognition as a distinct species: *Pseudomyrmex major* (Forel 1899:91), **stat. nov.** (syntype worker, Pinos Altos, Chihuahua, Mexico (Buchan-Hepburn) (BMNH) (examined); original combination: *Pseudomyrma gracilis* var. *major*). Workers of *P. major* can be distinguished from those of *P. gracilis* by their emarginate median clypeal lobe, less distinct anterior peduncle of the petiole, and larger average size. Males of *P. major* have broadened fore-tarsal segments. *P. major* is confined to western Mexico, where it occurs sympatrically with *P. gracilis* without show-

ing signs of intergradation.

Distribution and biology.—Befitting its wide distribution (southern United States to Argentina and Brazil) and variable phenotype, *P. gracilis* can be found in a variety of habitats from mangroves and thorn scrub to rainforest. It is often particularly common in disturbed situations such as old fields, roadsides, and secondary forest. Nests are usually located in dead twigs or small branches, but there are a substantial number of records of colonies occupying swollen-thorn acacias in Central America (Mexico to Panama). In a few localities *P. gracilis* is a common acacia inhabitant and under these circumstances it may exhibit local adaptation and phenotypic differentiation (see also Wheeler 1942:107). For example, Janzen collected a series of specimens from *Acacia gentlei* in Belize (15 mi. S Santa Elena) which have somewhat distinctive morphology: the workers are large, dark, abundantly hairy, and possess rather short petioles (PLI 0.55), although none of these features is outside the total range of variation for the species. Janzen (1974:98) notes that the workers of this large black morph have atypically aggressive behavior. Given the kind of ecotypic variation to which *P. gracilis* is prone, it is not surprising to find a tendency of some populations to specialize on acacias. The ecology of this species is reminiscent of other animal species which show broad ecophenotypic variation, e.g. fish with trophic polymorphisms (Kornfield et al. 1982; Grudzien and Turner 1984; Sandlund et al. 1992).

***Pseudomyrmex hesperius* Ward, sp. nov.**

(Fig. 4)

Holotype worker.—MEXICO Sinaloa: 15.9 mi. NE Concordia, Hwy. 40, 600m, 9.vi.1967, D. H. Janzen XVIII, ex *Acacia hindsii* (LACM). HW 0.66, HL 0.83, EL 0.36, PL 0.34, PH 0.26.

Paratypes.—Same data as holotype: series of 11 workers (BMNH, LACM, MCZC, MZSP, PSWC, USNM).

Additional non-type material.—MEXICO Sinaloa: 14 km. S Mazatlán, 18.vii.1965, R. R. Snelling, 15 workers (LACM, MCZC, PSWC).

Worker measurements (n=6).—HL 0.78-0.85, HW 0.65-0.69, MFC 0.028-0.043, CI 0.79-0.83,

REL 0.43-0.46, REL2 0.54-0.57, OOI 0.86-1.15, VI 0.75-0.82, FCI 0.043-0.062, SI 0.48-0.51, SI2 0.87-0.93, FI 0.41-0.45, PDI 0.84-0.95, MPI 0.053-0.066, NI 0.54-0.59, PLI 0.73-0.77, PWI 0.63-0.70, PPWI 1.41-1.56.

Worker diagnosis.—Small species (see above measurements) with elongate, subrectangular head and short eyes (REL 0.43-0.46, OI 0.61-0.65). Masticatory margin of mandible with five teeth, the fourth tooth (counting from the apex) separated by a gap of ca. 0.05 mm from the apicobasal tooth; MD8/MD9 0.70; third and fourth teeth small, contrasting with the large subapical and apical teeth (the latter ca. 0.032 and 0.055 mm in length, respectively); mesial tooth on basal margin situated slightly closer to apicobasal tooth than to proximal tooth (MD4/MD5 0.65); palp formula 5,3; median clypeal lobe short, its anterior margin straight to weakly convex, sharply rounded laterally; minimum distance between frontal carinae subequal to or less than basal scape width; frontal carinae diverging anteriorly and fusing with the antennal sclerites; pronotum laterally rounded, without humeral angles; in lateral profile the mesonotum and basal face of propodeum slightly inclined anteriorly, separated by a well developed metanotal groove (Fig. 4); basal face of propodeum rounding into the longer declivitous face, the latter somewhat concave in profile; petiole short, apedunculate, shaped as in Fig. 4, with a prominent triangular anteroventral tooth; in dorsal view petiole very broad anteriorly (PWI3 0.59-0.62); postpetiole broader than long, its anteroventral process small and inconspicuous. Mandibles finely striate; head punctulate on a smooth shining background, punctulae separated by one to several diameters on upper half of head, becoming denser towards the clypeus; mesosoma sublucid, with weak punctulate-coriarius sculpture; petiole, postpetiole and gaster shining, with very fine piligerous punctures. Standing pilosity common but short (< 0.10 mm) on most parts of body, lacking on outer faces of tibiae. Appressed pubescence widely distributed, moderately dense on abdominal tergite IV. Dark brown; mandibles, appendages and fronto-clypeal complex tending towards a lighter brown.

Taxonomic comments.—This is a taxonomically isolated species, not belonging to any of the

nine major species groups of *Pseudomyrmex* (see Ward 1989). The salient features of *P. hesperius* are small size (HW < 0.72), reduced mandibular dentition and palp formula, short truncate median clypeal lobe, short eyes (especially obvious in lateral view, such that OI > 0.60), short apedunculate petiole with a broad attachment to the propodeum (PW/3 0.60), punctulate head sculpture, subclad integument, and short standing pilosity. Some of these traits are shared with two other Mesoamerican *Pseudomyrmex*, *P. fervidus* (F. Smith) and a related undescribed species, but both of these are larger (HW > 0.70), with standing pilosity which is longer and more extensive (present on the outer faces of the tibiae).

Biology.—Although the type specimens of *P. hesperius* were collected from *Acacia hindsii* this species is not an obligate acacia inhabitant. The series from 14 km. south of Mazatlán was collected from dead branches of a woody plant, not *Acacia* (R. R. Snelling, pers. comm.).

***Pseudomyrmex ita* (Forel 1906) stat. nov.**
(Fig. 2)

Pseudomyrma sericea var. *ita* Forel 1906:230. Syntype workers, San Mateo, Costa Rica (P. Biolley) (MHNG) [Examined]. One syntype here designated LECTOTYPE.

Pseudomyrma sericea var. *acaciarum* Wheeler 1942:176. Syntype workers, Tumba Muerta Road, Panama (W. M. Wheeler) (LACM, MCZC) [Examined] **Syn. nov.**

Pseudomyrma sericea var. *acaciorum* Enzmann 1945:90. Syntype workers, Tumba Muerta Road, Panama (W. M. Wheeler) (MCZC) [Examined] [Objective synonym of *Pseudomyrma sericea* var. *acaciarum* Wheeler; Brown 1949:43].

Pseudomyrmex sericeus ita (Forel); Kempf 1972:223.

Worker diagnosis.—A medium-sized member (HW ca. 0.75–0.98) of the *P. sericeus* group, with large elongate eyes (REL 0.65), convex median clypeal lobe, subcontiguous frontal carinae (MFC 0.02), and palp formula of 6,4. Head longer than broad (CI 0.85). Basal face of propodeum shorter than declivitous face and meeting the latter at an

angle. Petiole short, high (PLI > 1.00), with sharp dorsolateral margins; in profile anterior and dorsal faces of petiole weakly differentiated, rounding sharply into the vertical posterior face (Fig. 2). Body with fine punctulate-coriarious sculpture, opaque. Standing pilosity very sparse; a pair of stout setae present on the pronotal humeri, petiole, and postpetiole. Dark brown-black, with lighter brown maculation variably present on the pronotum, petiole, postpetiole, fronto-clypeal complex, and appendages.

Taxonomic comments.—This is one of several species originally described as “varieties” of *P. sericeus* (Mayr). Workers of *P. ita* can be distinguished from those of *P. sericeus* by the angulate shape of their petiole, especially in lateral view (Fig. 2); the petiole of *P. sericeus* is subtriangular in profile, with more gently rounded edges.

Distribution and biology.—*P. ita* occurs from Mexico to Colombia, and typically inhabits dead twigs or branches of various woody plants. It has been collected from thorns of *Acacia cornigera* in Mexico and *A. collinsii* in Costa Rica and Panama.

***Pseudomyrmex kuenckeli* (Emery 1890)**
(Fig. 3)

Pseudomyrma kuenckeli Emery 1890:62. Syntype workers, queens, Alajuela, Costa Rica (A. Alfaro) (MCSN) [Examined].

Pseudomyrma kuenckeli var. *dichroa* Forel 1904:41. Syntype workers, Dibulla, Colombia (A. Forel) (AMNH, BMNH, MCSN, MHNG, NHMB, USNM) [Examined] [Synonymy by Kempf 1961:402].

Pseudomyrma kuenckeli var. *bierigi* Santschi 1932:412. Holotype worker, Juan Díaz, Panama (A. Bierig) (NHMB) [Examined] [Synonymy by Kempf 1961:402].

Pseudomyrma crenulata Enzmann 1945:84. Holotype worker, “Guernavaca”, Mexico (not in MCZC) [Not examined; but other *P. kuenckeli* workers in the MCZC from Cuernavaca, Mexico (Wheeler) evidently represent the source series] [Synonymy by Kempf 1961:402].

Pseudomyrmex kuenckeli (Emery); Kusnezov 1953:214.

Worker diagnosis.—A member of the *P. viduus* group, easily recognized by the shiny broad head (CI 1.12), short eyes (REL 0.46), flattened mesosoma, blocky petiole, and abundant pilosity (Fig. 3). For further description see Kempf (1961:402).

Distribution and biology.—This is a widely distributed but generally uncommon species, found from Mexico to Argentina and Brazil. *P. kuenckeli* appears to have a preference for nesting in large dead branches, in somewhat open or seasonally dry forest. Its association with ant acacias is sporadic at best and based upon two records from Costa Rica: Emery (1891:168) reported a single specimen collected by Alfaro from a swollen-thorn acacia, and Menozzi (1927b) recorded a collection by H. Schmidt from *Acacia "spadicigera"* (probably a misidentification of *A. collinsii*) near San José.

***Pseudomyrmex nigropilosus* (Emery 1890)**
(Fig. 7)

Pseudomyrmanigropilosa Emery 1890:62. Syntype workers, Liberia, Costa Rica (A. Alfaro) (MCSN, MHNG) [Examined].

Pseudomyrmex nigropilosus (Emery); Kempf 1958:453.

Worker diagnosis. With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head longer than broad (CI 0.84-0.90); anterior margin of median clypeal lobe convex, conspicuously protruding; dorsolateral margination of pronotum usually blunt; mesonotum more steeply inclined than basal face of propodeum; petiole relatively robust (PLI 0.69-0.77) with a short anterior peduncle (Fig. 7, 53); head and mesosoma densely punctulate to coriarius-imbricate, and subopaque; standing pilosity conspicuous on most of the body including the outer faces of the tibiae, consisting largely of black hairs, those on the petiole and propodeum long (> 0.20 mm) and curved. Color varying from concolorous orange-brown to bicolored orange and black to (western Mexico) predominantly black with orange mottling on the head, mesosoma, and appendages.

Taxonomic comments.—Among the *Pseudomyrmex* species recorded from swollen-thorn acacias, *P. nigropilosus* is easily identified by its elongate eyes and head (REL 0.55-0.59, CI 0.84-0.90), short petiole (PLI 0.69-0.77), and conspicuous black pilosity (Fig. 7). Kempf (1958) provides further descriptive details.

Distribution and biology.—*P. nigropilosus* is found from Nayarit, western Mexico to Guanacaste Province, Costa Rica, and is restricted to nesting in swollen-thorn acacias (including *Acacia collinsii*, *A. cornigera* and *A. hindsii*). It is a member of the *P. gracilis* group and therefore not closely related to the principal group of acacia-ants (*P. ferrugineus* group). Janzen (1975) points out that *P. nigropilosus* is essentially a parasite of the *Pseudomyrmex*/*Acacia* mutualism. It occupies abandoned or otherwise uninhabited plants and reaps the benefits of this association without protecting the acacia from herbivores or competing plants. Additional information about the ecology of this species is given in Janzen (1975).

***Pseudomyrmex opaciceps* Ward, sp. nov.**
(Fig. 5)

Holotype worker.—GUATEMALA *Retalhuleu*: Puente Samala, 3.8 mi. NE San Felipe, 24.vii.1966, D. H. Janzen W006724966 (LACM). HW 1.43, HL 1.42, EL 0.85, PL 0.89, PH 0.39.

Paratypes.—Series of 11 workers with same data as holotype; large series of ca. 60 workers and 10 males with the same locality and collector as holotype but the following dates and collection numbers: 18.vii.1966 M002718966 (possibly mislabelled - see below), 18.vii.1966 W002718966, 18.vii.1966 W004718966, 18.vii.1966 W005718966 (possibly mislabelled - see below), 23.vii.1966 W002723966, 24.vii.1966 W001724966, 24.vii.1966 W003724966 (BMNH, LACM, MCZC, MZSP, PSWC, UDCD, USNM).

Additional non-type material.—Series of workers, queens, and males from six additional localities. MEXICO *Chiapas*: 94.5 mi. SE Tonala (D. H. Janzen). GUATEMALA *Retalhuleu*: 2 mi. N Puente Samala, 3.8 mi. NE San Felipe (D. H. Janzen); 3 mi. N Puente Samala, 3.8 mi. NE San Felipe (D. H. Janzen); 5 mi. W Retalhuleu, Hwy. CA-2 at Rio Nil

(D. H. Janzen); *Guatemala*: Ciudad de Guatemala (D. H. Janzen). EL SALVADOR *La Libertad*: Quezaltepeque (M. Irwin & D. Cavagnaro) (LACM, MCZC, PSWC).

Worker measurements (n=14).—HL 1.30-1.42, HW 1.33-1.43, MFC 0.040-0.058, CI 0.99-1.04, REL 0.57-0.61, REL2 0.56-0.61, OOI 0.14-0.68, VI 0.65-0.71, FCI 0.029-0.042, SI 0.46-0.50, SI2 0.77-0.88, FI0.36-0.39, PDI 1.12-1.37, MPI0.059-0.076, NI0.65-0.70, PLI0.42-0.47, PWI0.38-0.43, PPWI 0.92-1.16.

Worker diagnosis.—With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head about as broad as long; anterior margin of median clypeal lobe straight to weakly convex; pronotum with blunt dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole long and slender (see PLI and PWI values) with a distinct anterior peduncle (Fig. 6); head densely punctulate-coriarious and matte; standing pilosity abundant, pale silvery-white, not black. Color: head and mesosoma dark brown to black, mandibles and appendages lighter brown; petiole, postpetiole and gaster a contrasting pale luteous brown or orange-brown. Portions of the fronto-clypeal complex, malar area, and mandibles may also be luteous brown.

Taxonomic comments.—This species is distinguished from the closely related and sympatric *P. gracilis* by a modest but consistent difference in head sculpture. In workers and queens of *P. opaciceps* the punctulate-coriarious sculpture and associated dense pubescence obscure the sheen of the head, producing a matte appearance under soft light, while in *P. gracilis* the head remains at least weakly shining. In addition the workers and queens of *P. opaciceps* average smaller in size than those of *P. gracilis* and they have a more slender petiole (PLI < 0.48; see Figs. 5, 6, 53). Finally, *P. opaciceps* has a distinctive and largely invariant color pattern: the pale yellow or orange-brown petiole, postpetiole and gaster contrast with the much darker head and mesosoma. This is not observed in Central American *P. gracilis*, although a similar color pattern occurs in some Colombian populations of *P. gracilis*, and it also seen in some individuals of the more distantly related South American species *P. venustus*

(F. Smith).

Among the *P. opaciceps* paratypes in LACM, the pinned specimens with Janzen collection numbers M002718966 and W005718966 appear to have been mis-labelled. In the Janzen alcohol collection samples M002718966 and W005718966 contain colony series of two quite different species (in the *P. ferrugineus* and *P. pallidus* groups, respectively); but there are two other alcohol samples from the same date and locality (W002718966 and W004718966) which are of *P. opaciceps*. I conclude that a frame-shift occurred in the process of labelling the pinned series of specimens, producing the labelling error (this has happened to a substantial number of *P. ferrugineus* group collections - see "Materials and Methods" section). The remaining paratype (and non-type) material of *P. opaciceps* appears to be correctly labelled.

Biology.—*P. opaciceps* is evidently a generalist twig-nesting *Pseudomyrmex*, but Janzen also collected it from an *Acacia conigera* tree overgrown by vines and unoccupied by the *P. ferrugineus* group (5 mi. W Retalhuleu, Guatemala, collection numbers M010714966-A and M010716966-D).

Pseudomyrmex reconditus Ward, sp. nov.

(Fig. 8)

Holotype worker.—NICARAGUA, *Madriz*: 2.0 mi. S Honduran border, Hwy 1, 840m, 29.vii.1967, mi. 8207.2, D. H. Janzen, ex *Acacia collinsii* (LACM).

Paratypes.—One worker, one dealate queen, same data as holotype (LACM).

Holotype and paratype worker measurements.—HL 1.54, 1.44, HW 1.54, 1.47, MFC 0.071, 0.056, EL 0.93, 0.86, PL 0.88, 0.78, PH 0.57, 0.47, CI 1.00, 1.02, OI 0.52, 0.52, REL 0.61, 0.59, REL2 0.61, 0.58, OOI -0.01, -0.01, VI 0.73, 0.71, FCI 0.046, 0.038, SI 0.47, 0.47, FI 0.44, 0.39, PDI 1.21, 1.12, MPI 0.067, 0.061, NI 0.62, 0.64, PLI 0.64, 0.60, PWI 0.57, 0.53, PPWI 1.40, 1.25.

Paratype queen measurements.—HL 1.79, HW 1.66, MFC 0.065, EL 1.02, PL 1.21, PH 0.75, CI 0.92, OI 0.51, REL 0.57, REL2 0.62, OOI 0.22, VI 0.79, FCI 0.039, SI 0.45, FI 0.46, NI 0.61, PLI 0.62, PWI 0.61, PPWI 1.53.

Worker diagnosis.—With the traits of the *P.*

gracilis group (see couplet 6 of key) and the following more specific features. Head as broad as long; anterior margin of median clypeal lobe slightly convex, rounded laterally; pronotum with blunt dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole of moderate length, high (PLI 0.60-0.64), with a distinct anterior peduncle but without a well developed anteroventral tooth (Figs. 8, 53), and lacking sharp dorsolateral margination; postpetiole notably broader than long. Mandibles weakly striolate, subclad, becoming shagreened basally; head and mesosoma densely but finely punctulate-coriarius to coriarius-imbricate, subopaque; petiole, postpetiole, and gaster with fine piligerous punctures, obscured from view by the associated pubescence. Standing pilosity only moderately dense but with some apparent loss due to abrasion of the type specimens; hairs mostly black, not silvery-white, present on the head, mesosoma dorsum, petiole, and postpetiole; at least some moderately long (0.23-0.27 mm) hairs on the propodeum and petiole; one or two short hairs present on the outer faces of the meso- and meta-tibiae, the others possibly worn off; fine appressed golden pubescence present on most of the body. Head and mesosoma black, gaster dark brown, petiole and postpetiole orange; appendages brown, with orange flecking on the legs.

Taxonomic comments. This species is known only from the types. It is readily distinguished from all other acacia-associated species in the *P. gracilis* group by the combination of broad head (see CI values), robust petiole (PLI 0.60-0.64), and black pilosity. *P. reconditus* is similar to an undescribed *Pseudomyrmex* species collected from *Tachigali* in northern Peru (*P. sp.* PSW-35) but the latter has a shorter petiole, more extensive silvery-white pilosity and pubescence, and is all black in color.

Biology.—The type collection from *Acacia collinsii* is the only record. A single worker of *P. nigropilosus* occurred in the same alcohol vial as the workers and queen of *P. reconditus*. It remains to be confirmed that *P. reconditus* is confined to nesting in swollen-thorn acacias.

Pseudomyrmex simulans Kempf 1958
(Fig. 9)

Pseudomyrmex simulans Kempf 1958:459. Holotype worker, Tumba Muerta Road, Panama (W. M. Wheeler) (MCZC) [Examined].

Worker diagnosis.—With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head longer than broad (CI 0.86-0.90); anterior margin of median clypeal lobe straight to broadly convex, rounded laterally; pronotum with sharp dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole relatively short and high (PLI 0.61-0.66), with a distinct anterior peduncle (Figs. 9, 53), and with moderate dorsolateral margination; head and mesosoma finely punctulate-coriarius to coriarius-imbricate, subopaque; standing pilosity rather short, pale and inconspicuous, present on the mesosoma dorsum and (usually) outer surfaces of the tibiae, but sometimes lacking or worn off on the latter; fine appressed pubescence on most of body; dark brown-black in color, distal portions of appendages lighter; mandibles luteous.

Taxonomic comments.—This curious species bears a superficial resemblance to the obligate acacia-ants (*P. ferrugineus* group), although its affinities to other *P. gracilis* group species are clear from eye size, pilosity, palp formula, mesosomal structure, and male genitalia. *P. simulans* can be recognized by the combination of elongate eyes (REL 0.52-0.55), short petiole (PLI 0.61-0.66), short inconspicuous pilosity, and black color.

Distribution and biology.—*P. simulans* is known only from a few collections, all from swollen-thorn acacias (*A. collinsii*), in Panama (Canal Zone and the provinces of Veraguas, Los Santos and Panamá). Nothing has been published about its nesting biology or behavior, but Janzen's field notes indicate that the workers are more timid than those of the *P. ferrugineus* group. One might surmise that its habits are similar to those of *P. nigropilosus*, although the two species do not appear to be one another's closest relatives (Ward 1991).

Pseudomyrmex subtilissimus (Emery 1890)

Pseudomyrma subtilissima Emery 1890:65. Lectotype worker, Alajuela, Costa Rica (Alfaro)

(MCSN) [Examined].

Pseudomyrmex subtilissimus (Emery 1890); Kempf 1972:224.

Worker diagnosis.—A member of the *P. subtilissimus* group, and immediately distinguishable from all other acacia-associated *Pseudomyrmex* by its small size (HW < 0.60), elongate head (CI < 0.66), apedunculate petiole, and scarcity of standing pilosity. See Ward (1989:432) for further discussion of this species.

Distribution and biology.—*P. subtilissimus* has been collected only in Nicaragua and Costa Rica. What little is known about its biology suggests that it is a timid, non-protective species living in the thorns of *Acacia* plants occupied by (declining?) colonies of *P. flavicornis*.

PHYLOGENY AND BIOGEOGRAPHY OF THE OBLIGATE ACACIA-ANTS

The 47-character data set used for cladistic analysis of the *P. ferrugineus* group is given in Table 2. Implicit enumeration by Hennig86, using the ie* command, yielded a single most parsimonious tree of length 73, consistency index 0.86 (0.84 excluding autapomorphies of ingroup species) (Fig. 73). This tree has an unresolved trifurcation involving five *Pseudomyrmex* species: *ferrugineus*, *janzeni*, and (*flavicornis* + (*mixtecus* + *veneficus*)). These five species together constitute what may be termed the *P. ferrugineus* complex. It is allied to the pair of sister species, *P. spinicola* and *P. satanicus*. The sister group of these seven species is the isolated and autapomorphic *P. peperii*. Finally, *P. nigrocinctus* and *P. particeps* make up a basal pair of species with relatively unspecialized morphology.

Separate analyses of worker-, queen-, and male-based data sets produced trees in substantial agreement with these findings and largely congruent with one another (Figs. 74–76). This indicates that some confidence can be attached to the main features of the cladogram, and that homoplasy in worker and queen morphology — possibly due to parallel selection pressures during diffuse coevolution of the ant/acacia interaction (see below) — has not been so rampant as to obscure all evidence of

relationship, since both castes point to a cladistic pattern similar to that derived from male morphology (primarily male genital characters). Disagreement revolves around the position of taxa within the *P. ferrugineus* complex. Worker morphology suggests that *P. mixtecus* is more closely related to *P. flavicornis* than to *P. veneficus*. The male character set supports a (*P. mixtecus* + *P. veneficus*) pairing and is uninformative about other relationships within the *P. ferrugineus* complex. The queen-based tree is identical in topology to that based on all characters, i.e. it supports (*P. flavicornis* + (*P. mixtecus* + *P. veneficus*)) but does not resolve relationships among *P. ferrugineus*, *P. janzeni*, and the foregoing trio.

The inferred phylogeny of the *P. ferrugineus* group (Fig. 73) suggests that speciation has occurred primarily as a consequence of geographical isolation. Of the three pairs of sister species, two (*P. nigrocinctus* + *P. particeps*, *P. mixtecus* + *P. veneficus*) are composed of allopatric species (Figs. 69, 72), while the ranges of the third pair (*P. spinicola* and *P. satanicus*) are more or less contiguous (Fig. 68). The trio of species comprising (*P. flavicornis* + (*P. mixtecus* + *P. veneficus*)) also have entirely non-overlapping distributions, and they point to the importance of geographical barriers in southwestern Mexico to speciation in this complex (Fig. 69). This is also indicated by the distributions of *P. ferrugineus* and *P. janzeni*, the latter an allopatric isolate in western Mexico (Fig. 70), although it should be noted that the cladistic analysis did not confirm a sister group relationship between these two phenetically similar species. At higher levels in the cladogram there is some geographical overlap between taxa, but dispersal has not been so extensive as to obliterate all evidence of vicariance. Within the *P. ferrugineus* complex, for example, *P. flavicornis* and relatives are largely confined to the Pacific slopes of Mesoamerica in contrast to the more eastern distribution of *P. ferrugineus* (Figs. 69–70). The *P. ferrugineus* complex itself is centred in northern Central America, with only one species (*P. flavicornis*) occurring south of Honduras, as far as Costa Rica in this case, while its sister group (*P. spinicola* and *P. satanicus*) occurs primarily south of Honduras and extends all the way to northern Colombia (Fig. 68). This suggests an historical barrier somewhere in the region of present day

Honduras or Nicaragua which split these two clades. The most basal divisions within the *P. ferrugineus* group involve much more extensive geographical overlap, making any historical inferences difficult. The distributions of the species *P. peperi* and *P. nigrocinctus* are consistent with an origin and early diversification of the *P. ferrugineus* group in either northern or central Mesoamerica. The timeframe for this is unknown but presumably occurred prior to the formation of the Panamanian land bridge (i.e. before early Pliocene or late Miocene). Early diversification in the group may have been encouraged by the presence of an island archipelago in the region (Donnelly 1992).

Finally, we come to the question of whether the phylogenies of the acacia-ants and their host acacias are congruent. A phylogeny of the swollen-thorn acacias is not available but Janzen's (1974) revision contains some relevant information. Janzen (1974) concluded that the Central American swollen-thorn acacias are polyphyletic, i.e. that myrmecophytism arose more than once or that non-mymecophytic acacia species independently acquired myrmecophytic traits through hybridization. He also noted (Janzen 1966) that individual species of acacia can be associated with more than one *Pseudomyrmex* species and vice versa. None of

this leads one to expect a pattern of co-speciation, and mapping known host associations on the *Pseudomyrmex* cladogram (Fig. 73) confirms the opportunistic nature of the interaction. It seems that most species in the *Pseudomyrmex ferrugineus* group occupy any swollen-thorn acacia species available to them. On the other hand, the possibility of locally non-random associations between ants and available plants, perhaps mediated by competition, deserves investigation.

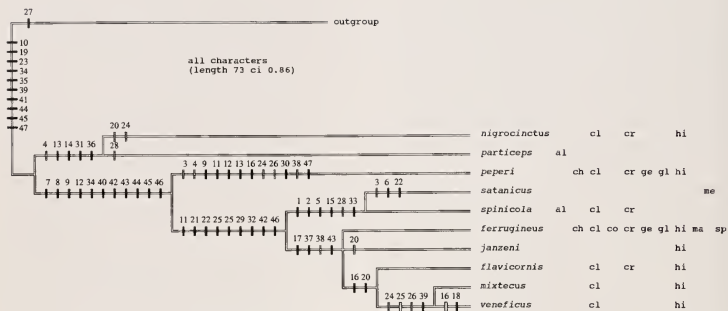
Three species of acacia-ants, *P. janzeni*, *P. particeps* and *P. satanicus*, are confined to a single acacia species (*A. hindsii*, *A. allenii* and *A. melanoceras*, respectively), the former (*P. janzeni*) almost certainly because of its limited geographical distribution but the last two because of their apparent specialization on the acacia or the forest habitat to which it is restricted. Populations of other swollen-thorn acacia species occur within the probable dispersal ranges of alate queens of *P. particeps* and *P. satanicus* but are apparently not colonized. These two host-specific *Pseudomyrmex* have the smallest ranges of any members of the *P. ferrugineus* group and are clearly the most endangered.

CONCLUDING REMARKS

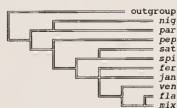
Table 2. Data set used for cladistic analysis of the *Pseudomyrmex ferrugineus* group. *P. fervidus* served as outgroup (see text). "?" signifies polymorphism or ambiguity in expression of the character state. Characters 12, 13 and 16 were considered unordered.

	1	11	21	31	41
<i>fervidus</i>	0000000000	?000000001	?000?00000	0000000000	00000?0
<i>nigrocinctus</i>	0001000001	1021000010	0011001000	0001110010	1001101
<i>particeps</i>	0001000001	1021000011	0010001100	0001110010	1001101
<i>peperi</i>	0011001121	2210020011	0011011001	0002100111	1112212
<i>spiniola</i>	1100101111	010010001?	1110?01110	0112100011	1212221
<i>satanicus</i>	1110111111	0100100011	1210201110	0112100011	1212221
<i>ferrugineus</i>	0000001111	0100001011	1110201010	0102101111	1222221
<i>janzeni</i>	0000001111	0100001010	1110201010	0102101111	1222221
<i>flavicornis</i>	0000001111	0100011012	1110201010	0102101111	1222221
<i>mixtecus</i>	0000001111	0100011012	1111111010	0102101121	1222221
<i>veneficus</i>	0000001111	0100001112	1111111010	0102101121	1222221

73



74

worker characters
(length 29 ci 0.89)

75

queen characters
(length 33 ci 0.75)

76

male characters
(length 28 ci 0.96)

Figs 73-76. Phylogenetic relationships of the obligate acacia-ants, *Pseudomyrmex ferrugineus* group. 73: cladogram based on the entire 47-character data set (Table 2), with character state changes indicated and with host plant associations listed for each species. Solid bars: unique forward changes; hatched bars: homoplasious forward changes; open bars: reversals. There are alternative, equally parsimonious reconstructions of character state change for characters 4, 12, 16, 38 and 46. By reference to other *Pseudomyrmex* species, most changes occurring between the outgroup (*P. fervidus*) and the ingroup (i.e. changes in characters 10, 19, 23...47) are probably synapomorphies of the latter, but one character state (27.0) appears to be a derived feature of *P. fervidus*. The following abbreviations are used for host plants: al = *Acacia allenii*, ch = *A. chiapensis*, cl = *A. collinsii*, co = *A. cooki* and *A. janzenii*, cr = *A. cornigera*, ge = *A. gentilei*, gl = *A. globulifera*, hi = *A. hindsii*, ma = *A. mayana*, me = *A. melanoceras*, sp = *A. sphaerocephala*. 74-76: cladograms based on the worker, queen and male character sets, respectively.

This systematic study of *Pseudomyrmex* ants associated with swollen-thorn acacias in Central America demonstrates that the primary group of obligate acacia-ants (the *P. ferrugineus* group) is monophyletic and comprises 10 species. Four additional unrelated *Pseudomyrmex* species, from two other species groups, have become secondary specialists on the acacias. These latter species appear to be parasites or commensals but little is known about their biology (except *P. nigropilosus*). These 14 specialists are joined by at least six generalist twig-nesting *Pseudomyrmex* which occasionally colonize acacia thorns.

The well known mutualism between ants and Central American acacias applies with certainty only to members of the *P. ferrugineus* group and their associated plants. Within this group experimental evidence of a mutualism is available only for the *P. ferrugineus* x *A. cornigera* interaction (Janzen 1966, 1967b), although the biology and behavior of the other nine species of ants suggest that they also provide important protection to their host acacias under most conditions. Cladistic analysis of the *P. ferrugineus* group, coupled with a consideration of host plant associations, indicates a pattern of diffuse coevolution, not one-on-one cospeciation (see also Janzen 1966). It seems likely that the original obligate acacia-ant (the common ancestor of the *P. ferrugineus* group) underwent coevolution with its acacia host, but since then speciation and diversification of the two groups have been decoupled — the swollen-thorn acacias are apparently even polyphyletic (Janzen 1974) — and there has been much opportunistic pairing of ants and plants. Such liberal sharing of partners has presumably made the association susceptible to invasion by other *Pseudomyrmex* and *Acacia* lineages.

At the same time the key features of the system — absolute dependence of ants in the *P. ferrugineus* group on acacia plants, the reliance of at least some (probably most) of the swollen-thorn acacia species on ants for normal growth and reproduction, and the suite of mutually beneficial traits exhibited by both partners — mark this as one of the more impressive insect/plant mutualisms known.

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**Species of *Orasema* parasitic on the *Solenopsis saevissima*-complex
in South America (Hymenoptera: Eucharitidae, Formicidae)**

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Abstract.— The South American species of the *Orasema xanthopus*-group are revised. The five species included are *O. pireta* n. sp., *O. salebrosa* n. sp., *O. simplex* n. sp., *O. worcesteri* (Girault) (*O. doellojuradoi* Gemignani as new synonym), and *O. xanthopus* (Cameron) (*Eucharomorpha paraguayensis* Girault and *O. crassa* DeSantis as new synonyms). Immature stages are described for three of the species. Ant hosts include *Pheidole radoszkowskii* Mayr, *Solenopsis invicta* Buren and *Solenopsis richteri* Forel (all Myrmicinae). The life history of *O. xanthopus* is discussed.

Several reports have mentioned a species of *Orasema* (Hymenoptera: Eucharitidae) that is a parasite of fire ants in South America (Silveira-Guido et al. 1964; Williams and Whitcomb 1973; Williams 1980; Wojcik 1988, 1989; Wojcik et al. 1987). These parasites are dominant among the insect parasites of fire ants in Brazil and, in 1585 collections of colonies from Brazil, represented about 80% of all myrmecophilous arthropods recovered (Wojcik et al. 1987). Parasites of ants in the *Solenopsis saevissima*-complex, revised by Trager 1991, all belong to a single species group of *Orasema* that occurs over the same range as the host complex in South America.

Almost all species of *Orasema* are parasites of Myrmicinae (Formicidae) and are known to parasitize ants in the genera *Pheidole*, *Solenopsis*, *Tetramorium* and *Wasmannia* (Heraty in press-b). Females deposit a single egg into a chamber formed in leaf tissue using a specialized ovipositor (Johnson et al. 1986, Heraty in press-a,b). The first-instar larvae reach the ant nest by some means of phoretic behaviour, either through attachment to an ant or to an intermediate insect host, and then parasitize the host larva (Johnson et al. 1986, Heraty in press-a,b). Development is completed on the pupal stage of the host.

Collections of colonies of *Solenopsis invicta* Buren from Bolivia and Brazil, and *Solenopsis richteri* Forel from Argentina, have permitted for study of the immature stages of three species, and

these are described here. The life histories and structures of the immature stages do not differ greatly from those first described by Wheeler (1907) for other species of *Orasema*; however, differences in structure at the species level do exist. Within this species-group of *Orasema*, the oviposition habits, plant host, and behavior of planidia outside of the host colony remain largely unknown. This paper provides diagnoses and correct nomenclature, and summarizes the distribution and biology for species of *Orasema* that are known to be parasites of fire ants of South America.

The terms used in the descriptions follow Heraty (1989, in press-a). Museum acronyms are described in the acknowledgements.

***Orasema xanthopus*-group**

The five species included in the *xanthopus*-group have the following combination of character states: funicle 8-segmented, scape yellowish brown, face and mesoscutum reticulate, and axillular sulcus at least partially discernible. The hind femora is dark brown to black medially in all included species, but sometimes not in all specimens of each species; however, this combination of a darkened femora with the other character states listed above is unique among *Orasema*. This group of species may be paraphyletic with respect to a monophyletic group that includes *Orasema aenea* (Gahan), which is distinguished by: mesosomal dorsum coarsely

rugose, axillular sulcus absent, and femora always completely yellowish brown. **Group Description** [diagnostic characters in bold type]. Colour of head, mesosoma, coxae and petiole usually dark (rarely bright) olive- or bluish-green, sometimes with red or purple iridescent patches; gaster dark brown with bluish green reflections; **scape yellowish brown**, with following segments, including pedicel and anellus, brown; **all femora usually at least slightly darker medially** with apices yellowish brown, rarely completely yellowish brown, tibiae yellowish brown. Wings hyaline, veins light brown.

Head 1.2-1.5X as broad as high; occiput broadly emarginate in dorsal view. **Face, including scrobal depression, finely reticulate**; scrobes shallow and narrowed medially (Figs. 1-5), median ocellus partially included; toruli separated by distance equal to their diameter; occiput aciculate, dorsal margin without carina but angle sharp at vertex. Eyes bare. Clypeus transverse and distinctly shorter than supraclypeal area, apical margin of clypeus nearly straight, lateral margin deeply impressed at tentorial pit; frontogenal sulcus meeting torulus at outer margin. Malar depression weakly impressed adjacent to oral fossa. **Labrum with 4 long digits**. Mandibles 3/2 dentate; maxillary palpus with 3 segments, labial palpus with 2 or 3 segments. Antenna with 12 segments; anellus distinct; **funicle in both sexes with 8 segments**; clava subconical and

rounded apically.

Mesosoma with **midlobe of mesoscutum reticulate**, and side lobe with similar but weaker sculpture dorsally. Notaulus and scutoscutellar sulcus deeply impressed and crenulate. Axillular sulcus at least weakly indicated. Disc of propodeum evenly sculptured. Transepimeral sulcus distinct; mesepisternum evenly reticulate except for anterior and ventral regions. Prepectus triangular. Proepisternum weakly sculptured. **Hind coxa reticulate dorsally**. Fore wing 2.2-2.6X as long as broad and broadly rounded apically; **basal area bare except for setae along impression of cubital vein**, costal cell pilose, **speculum present** and closed basally, disc pilose and hyaline with prominent marginal fringe; stigmal vein angled slightly towards apex of wing; postmarginal vein 2-4X as long as stigmal vein.

Petiole of female 0.8-1.0X as long as hind coxa, that of male 1.0-1.4X as long as hind coxa; **petiole smooth, weakly rugose (wrinkled) or finely reticulate**, cylindrical with basal flange usually weak. First gastral sternite (Ms^2) with transverse crenulate sulcus. Ovipositor expanded subapically; first valvula with lateral line of 4 to 10 prominent teeth distal to subapical ridge; second valvula broad with 7-9 lateral teeth, and with or without weak transverse ridges. Genitalia typical for genus; basiparamere robust and broad, paramere short and well sclerotized, aedeagus subtruncate.

KEY TO SPECIES OF THE *ORASEMA XANTHOPUS*-GROUP

1. Petiole finely and strongly reticulate *worcesteri* Girault
— Petiole smooth, weakly rugose, or carinate (if present, rugae smooth and hardly raised above surface) 2
2. Petiole of female 2.6-3.1X as long as broad, completely smooth with 1 or 2 longitudinal carinae basally; mesepimeron and callus smooth; callus with prominent nib (male unknown) ... *pireta* Heraty, n. sp.
— Petiole of female 1.3-2.0X as long as broad, petiole of both sexes weakly rugose or carinate; mesepimeron and callus usually with prominent sculpture, callus without nib 3
3. Scutellum scabrous dorsally; callus rugulose and with 10-12 prominent hairs
— Scutellum finely reticulate dorsally; callus coriaceous or mostly smooth and with 2-4 minute hairs or bare 4
4. Axillular sulcus indistinct, at most vaguely indicated by change in sculpture; dorsal margin of scutellum flat in profile; femora of both sexes mostly dark brown to black ... *simplex* Heraty, n. sp.
— Axillular sulcus distinct and foveate, at least anteriorly; dorsal margin of scutellum rounded in profile; femora of female weakly to strongly darkened medially, that of male weakly darkened or completely yellowish brown *xanthopus* (Cameron)

Orasema pireata Heraty, new species

(Fig. 1)

Holotype, female "PARAGUAY: Pirareta, 26.xii.1971, L.E. Peña." Deposited in CNC.

Paratypes: PARAGUAY: same data (2 females, CNC; 1 female, USNM); same locality and collector, 23-25.xii.1971 (1 female, CNC).

Diagnosis.—Within the *xanthopus*-group, recognized by: petiole narrow and elongate, 2.6-3.1X as long as broad, and mostly smooth and shining with at most with few weak longitudinal carinae in basal third; mesepimeron, callus and metepimeron smooth; callus with 2-3 minute setae and with prominent calar nib; femora of female completely yellowish brown or weakly fuscate medially; axillular sulcus strongly impressed.

Description of female.—Length, 3.0-3.9 mm. Colour of head and body dark brown with greenish-blue reflections, strongest on head and mesosomal dorsum [may be partially bleached in these specimens].

Head 1.3-1.4X as broad as high (Fig. 1). Facial sculpture reticulate with interstices hardly raised above surface, intertorular area smooth. Eyes separated by 1.8X their height. Malar space 0.8-0.9X height of eye. Clypeus and supraclypeal area swollen medially, clypeus smooth with few small setae. Flagellum 1.6-1.7X height of head; FL2 1.1-1.4X as long as broad.

Mesosoma with entire dorsum finely reticulate, side lobe of mesoscutum alutaceous. Disc of scutellum slightly longer than broad, flat dorsally (in lateral view), and without median depression; frenum finely reticulate; frenal line broadly and deeply impressed dorsally, strongly angled to scutellar disc (in lateral view), and reticulate dorsally and glabrous laterally; axillula vertical and smooth or with weak rugosity, axillular sulcus strongly impressed and reticulate. Propodeal disc weakly reticulate or alutaceous laterally and with broad median areolate depression; callus swollen and smooth, with 2-3 minute hairs dorsally or bare, and with prominent callar nib. Mesepimeron smooth. Fore wing 2.3-2.5X as long as broad.

Petiole 1.3-1.5X as long as broad, 0.6-0.8X as long as hind coxa; petiole entirely smooth, sometimes with few weak longitudinal carinae in basal

third, the basal flange weak. First valvula of ovipositor with lateral line of 4 to 7 prominent teeth; second valvula with 7 lateral teeth connected by weak transverse ridges.

Male.—Unknown.

Host and immature stages.—Unknown.

Etymology.—Adapted from the name of the type locality.

Orasema salebrosa Heraty, new species

(Figs. 2, 19)

Holotype, female "ARGENTINA: Buenos Aires P., San Carlos de Bolivar, RN-226, 8.iv.1987, D.P. Wojcik 87-A-407, ex: floated fire ants." Deposited in CNC.

Paratypes: ARGENTINA: *Buenos Aires Prov.*: same data as holotype (1 female, CNC); Suipacha, RN-5, km 127, 28.x.1987, D.P. Wojcik, 87-A-590, ex: floated *Solenopsis richteri* (1 female, 1 male, 4 female pupae, CNC; 1 female, USNM); San Carlos de Bolivar, RN-226, 8.iv.1987, D.P. Wojcik, 87-A-407, ex floated fire ants (1 female, CNC).

Diagnosis.—Within the *xanthopus*-group, both sexes recognized by: side lobe of mesoscutum laterally, and scutellum dorsally, scabrous (rugose with interstices strongly raised and sharp); callus rugose with 10-12 hairs dorsally; femora of both sexes dark brown to black medially; axillular sulcus strongly impressed.

Description of female.—Length, 3.0-3.9 mm. Colour of head and body dark bluish green to almost black, sometimes with strong purple reflections laterally.

Head 1.3-1.4X as broad as high (Fig. 2). Face strongly reticulate, intertorular area transversely strigate. Eyes separated by 1.8X their height. Malar space 0.8-0.9X height of eye. Clypeus slightly swollen medially and mostly smooth with moderately dense fine setae. Flagellum 1.6-1.7X height of head; FL2 1.1-1.4X as long as broad.

Mesosoma with mesoscutum and axilla reticulate, scutellum rugose or scabrous, with interstices sharp. Disc of scutellum slightly longer than broad, flat dorsally (in lateral view), and with broad median depression; frenum rugose; frenal line strongly impressed and foveate or crenulate dorsally, glabrous laterally; axillula slightly rounded and rug-

ose, axillular sulcus strongly impressed and foveate. Propodeal disc evenly rugose-areolate, without median depression; callus swollen and rugose, with 10-13 hairs dorsally, and without callar nib. Upper mesepimeron swollen and weakly reticulate, lower mesepimeron rugulose. Fore wing (Fig. 5) 2.3-2.5X as long as broad.

Petiole 1.3-1.5X as long as broad, 0.6-0.8X as long as hind coxa; petiole smooth with weak irregular rugae, the basal flange weak. First valvula of ovipositor with lateral line of 8 prominent teeth [second valvula hidden].

Description of male.—Length, 3.1 mm. Eyes separated by 1.8X their height. Malar space 0.8X height of eye. Flagellum slightly longer than in female, 2.2X height of head. Fore wing 2.3X as long as broad. Petiole 2.7X as long as broad, 1.1X as long as hind coxa.

Host.—*Solenopsis richteri* Forel (Myrmicinae).

Immature Stages.—Pupa (Fig. 19). Pupal form is typical for other *Orasema* and recognized by: two enlarged tubercles over petiole, third enlarged tubercle further back over first metasomal tergite; gaster with series of small mid-dorsal tubercles,

decreasing in size, over terga II-V; series of small lateral and subventral tubercles or short ridges on terga I-VI. Average length, 3.67 mm (SD=0.48, n=5).

Etymology.—From Latin *salebrosus* for rough, referring to scutellar sculpture.

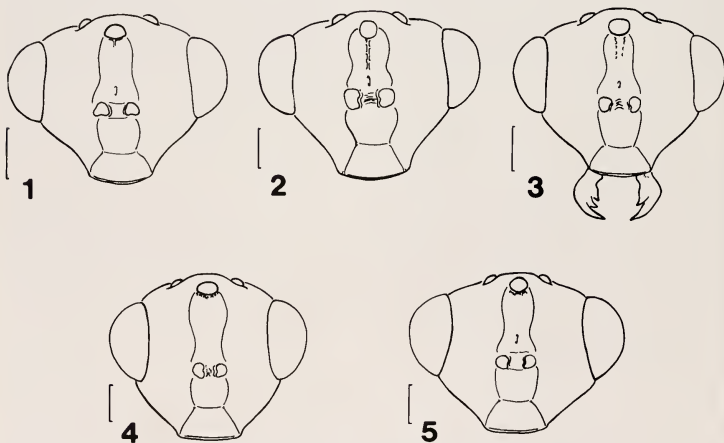
Orasema simplex Heraty, new species

(Fig. 3)

Holotype, female "ARGENTINA: Buenos Aires P., RN-9, km 231, jct San Nicolas de los Arroyos" "22.x.1987, D.P. Wojcik 87-A-552-D, ex: floated *Solenopsis richteri*." Deposited in CNC.

Paratypes: ARGENTINA: Buenos Aires: same data (1 male, 1 female pupa, CNC; 1 female, 1 male, USNM); Belen de Escobar, RN-9, km 51, 19.x. 1987, D.P. Wojcik, 87-A-483-H, ex: floated *Solenopsis richteri* (1 female pupa, CNC); La Pampa: 9.ix.1987, N. Puelen (2 females, CNC, NMBA).

Diagnosis.—Within the *xanthopus*-group, both sexes recognized by: frons and mesosomal dorsum very finely reticulate; scutellum flat dorsally,



Figs. 1-5. Head of female. 1, *O. pireta*. 2, *O. salebrosa*. 3, *O. simplex*. 4, *O. worcesteri*. 5, *O. xanthopus*.

axillular sulcus weakly impressed, discernable only by change in sculpture; mesepimeron and callus weakly and finely reticulate, and callus bare; petiole smooth with weak and irregular longitudinal rugae; femora of both sexes mostly dark brown or black.

Description of female.—Length, 2.7–3.8 mm. Colour of head and body bright green to dark greenish-blue, sometimes with reddish iridescent patches on mesosoma.

Head 1.3–1.4X as broad as high (Fig. 3). Face strongly reticulate, intertorular area transversely strigate. Eyes separated by 1.7–2.0X their height. Malar space 0.8–0.9X height of eye. Clypeus swollen medially and coriaceous, covered with moderately dense fine setae. Flagellum 1.3–1.4X height of head; FL2 1.3–1.7X as long as broad.

Mesosoma with entire dorsum finely reticulate. Disc of scutellum slightly longer than broad, flat dorsally (in lateral view), and with weak median depression; frenal line not impressed dorsally, forming a continuous glabrous band; axillula vertical and longitudinally strigate; axillular sulcus weakly impressed, visible as weak ridge in dorsal view or by change in sculpture. Propodeal disc weakly reticulate or coriaceous, with broad median rugose-areolate depression; callus swollen, weakly reticulate and bare, with weak callar nib. Upper mesepimeron swollen and weakly reticulate, lower mesepimeron mostly smooth. Fore wing 2.1–2.4X as long as broad.

Petiole 1.6–2.0X as long as broad, 0.7–0.8X as long as hind coxa; petiole smooth with weak irregular rugae, the basal flange weak. First valvula of ovipositor with lateral line of 9–10 prominent teeth; second valvula with 11 lateral teeth connected by weak transverse ridges.

Description of male.—Length, 2.7–3.0 mm. Eyes separated by 1.8–1.9X their height. Malar space 0.8X height of eye. Flagellum slightly longer than in female, 1.6X height of head. Fore wing 2.2–2.4X as long as broad. Petiole 2.8–4.1X as long as broad, 1.0–1.4X as long as hind coxa.

Host.—*Solenopsis richteri* Forel (Myrmicinae).

Immature Stages.—Pupa. Form is the same as for *O. salebrosa*, but the lateral tubercles are usually connected by a raised ridge that extends almost

to mid-dorsal series (ridge absent in one specimen and complete in another). Length, 3.4 mm.

***Orasema worcesteri* (Girault)**

(Fig. 4)

Eucharomorpha worcesteri Girault, 1913[157]: 62–63. Type locality: Paraguay, San Bernardino. Holotype, female [examined, ZMHB], by original designation.

Orasema Doello-juradoi Gemignani, 1933: 490–491, figs. 13–14. Type locality, Argentina: Isla Martin Garcia. Holotype, female [examined, NMBA, type no. 31765], by original designation; holotype, paratype and 2 ants mounted on three cards on same pin. The holotype is here assumed to be the top card-mounted specimen.

New Synonymy.

Orasema worcesteri; combination by Bouček, 1988: 519.

Diagnosis.—Within the *xanthopus*-group, female recognized by: femora usually all yellow, sometimes dark brown medially; head subquadrate (Fig. 4); frons and mesosomal dorsum very finely reticulate; scutellum flat dorsally, axillular sulcus weak; mesepimeron and callus weakly and finely reticulate, and callus bare; petiole finely and strongly reticulate with a weak basal flange, petiole shorter than length of hind coxa and 1.4–1.6X as long as broad. This species is similar to *O. simplex*, but differs by having a finely reticulate petiole, which is a unique character state among species with an 8-segmented funicle and a finely reticulate mesosomal dorsum.

Description of female.—Length, 2.8–4.0 mm. Colour of head and body bright green to dark greenish-blue, sometimes with reddish iridescent patches on mesosoma.

Head 1.2–1.3X as broad as high (Fig. 4). Face strongly reticulate, intertorular area rugulose. Eyes separated by 1.4–1.7X their height. Malar space 0.7–0.8X height of eye. Clypeus weakly sculptured or smooth and only slightly rounded medially. Flagellum 1.0–1.4X height of head; FL2 2.0–2.2X as long as broad.

Mesosoma with entire dorsum finely reticulate to granulate. Disc of scutellum 1.2X as long as broad, rounded dorsally (in lateral view), and with-

out median furrow; frenum granulate; frenal line impressed, reticulate dorsally and glabrous laterally; axillula vertical and weakly reticulate or striate, axillular sulcus weakly impressed, marked by difference in sculpture. Propodeal disc finely reticulate laterally, sometimes with broad median alveolate channel; callus reticulate and bare, callar nib absent. Upper mesepimeron weakly reticulate, lower mesepimeron smooth to areolate. Fore wing 2.3-2.5X as long as broad.

Petiole 1.4-1.6X as long as broad, 0.7-1.0X as long as hind coxa; petiole strongly reticulate over entire surface, the basal flange weak. First valvula of ovipositor with lateral line of 4 prominent teeth; second valvula broad with 9 lateral teeth connected dorsally by weak transverse ridges.

Male.—Unknown.

Host and Immature Stages.—The host was originally reported as *Pheidole nitidula* Emery (Gemignani, 1933). E.O. Wilson identified the same specimens as *Pheidole radoszkowskii* Mayr (Myrmicinae). Immature stages unknown.

Material Examined.—ARGENTINA: *Buenos Aires*: San Fernando, xi.1957, Daguerre (1 female, USNM); *Catamarca*: Sumalao, 30.i-5.ii.1958, R. Golbach; *Chaco*: Resistencia, M.V. Viana (1 female, NMBA); *Misiones*: Dept. Concepción, Santa Maria, 1948, M.J. Viana (3 females, NMBA); no city or date (1 female, NMBA); [province?] Amaicha del Valle, 28.xii.1965, H. & M. Townes (1 female, NMBA). PARAGUAY: *Caaguazú*: Estancia Primera, 1.xii.1931 R.F. Hussey (1 female, homotype of *O. worcesteri*, MMZ).

***Orasema xanthopus* (Cameron)**
(Figs. 5, 6-18)

Semora xanthopus Cameron, 1909: 433. Type locality: Argentina, Mendoza. Lectotype, female [examined, BMNH, type number 5.369], here designated. Labels: "Type" "P. Cameron Coll. B.M. 1914-110." "*Semora xanthopus* Cam Type Mendoza" "B.M. TYPE HYM 5.369."

Semorata xanthopus: replacement name by Strand 1942, *Semora* preoccupied by Peckham, 1892.

Semorella xanthopus: unjustified replacement name by Ghesquière, 1946: 368.

Orasema xanthopus: combination by Kerrich, 1963: 36.

Eucharomorpha paraguayensis Girault, 1913: 63. Type locality: Argentina, Mendoza. Holotype, male [examined, ZHMB], monotypic. Labels: "Argentina 4.2., Mendoza 07, Jansen Haarpur V" "*Eucharomorpha paraguayensis* Girault male" "S.M.I. Pv. 1045" "ex coll./Girault" "Zool. Mus./Berlin." A slide of an antenna of the holotype, as mentioned in the original description, was not examined. The type locality, Mendoza, was taken from holotype label data; the published locality of San Bernardino (Paraguay) is an error. **New synonymy.**

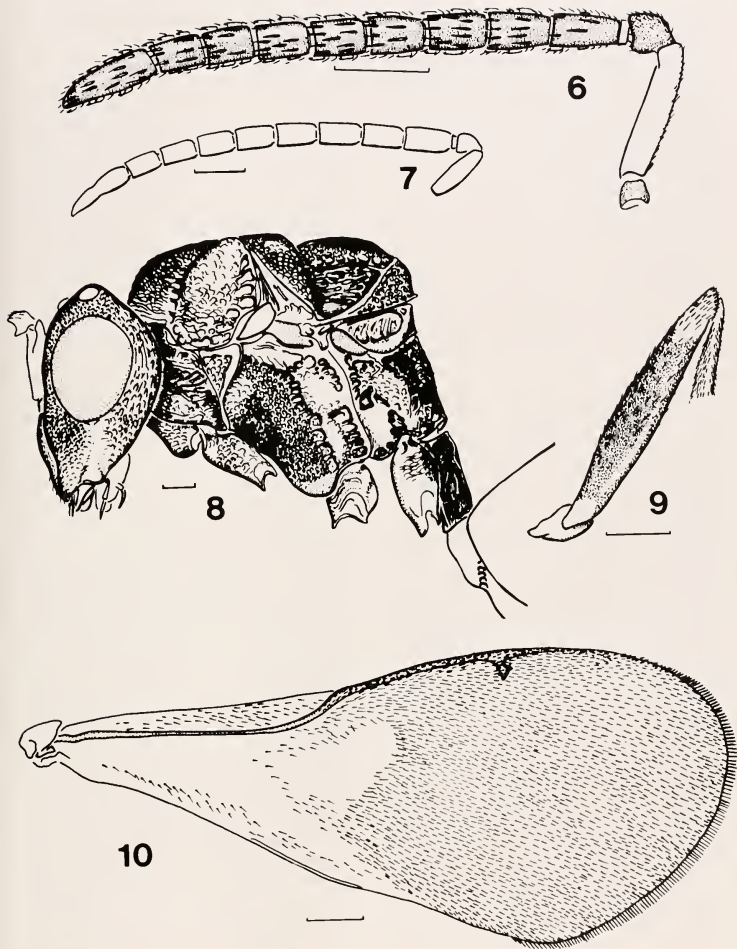
Orasema crassa De Santis, 1968: 3, fig. 1. Type locality: Uruguay, Canelones. Holotype, female [examined, FCNM, type number Za-201], originally designated. **New synonymy.**

Diagnosis.—Within the *xanthopus*-group, both sexes recognized by: frons and mesosomal dorsum finely reticulate; scutellum rounded dorsally (in lateral view) (Fig. 8), axillular sulcus strongly impressed and foveate, at least in basal half; mesepimeron and callus mostly smooth, callus with only few minute setae or bare; petiole smooth with weak and irregular longitudinal rugae; femora of female weakly to strongly fuscate medially (Fig. 9), that of male weakly fuscate or completely yellowish brown

Description of female.—Length, 2.9-3.5 mm. Colour of head and body usually dark (rarely bright) olive or bluish green, sometimes with reddish or stronger bluish reflections.

Head 1.3-1.5X as broad as high (Fig. 5). Face strongly reticulate, intertorular area smooth. Eyes separated by 1.7-1.9X their height. Malar space 0.8-0.9X height of eye. Clypeus and supraclypeal area coriaceous and slightly swollen medially. Flagellum 1.3-1.6X height of head; FL2 1.7-2.2X as long as broad (Fig. 6).

Mesosoma with dorsum finely reticulate, sometimes with overlay of irregular alveolate sculpture on midlobe and/or scutellum. Disc of scutellum slightly longer than broad, rounded dorsally (in lateral view) (Fig. 8), and without median furrow; frenum reticulate; frenal line deeply impressed



Figs. 6-10. *Orasema xanthopus*. 6, antenna of female. 7, antenna of male. 8, head and mesosoma of female. 9, hind femur of female. 10, fore wing of female. Scale bars represent 0.2 mm.

dorsally, reticulate dorsally and glabrous laterally; axillula vertical and weakly reticulate, striate or smooth; axillular sulcus strongly impressed and foveate, sometimes weakly impressed posteriorly. Propodeal disc reticulate laterally, with or without median longitudinal depression; callus swollen and weakly reticulate, at most with 2-3 minute setae dorsally, callar nib present or absent. Upper mesepimeron swollen and weakly reticulate, lower mesepimeron smooth to areolate. Fore wing 2.2-2.4X as long as broad (Fig. 10).

Petiole 1.5-2.4X as long as broad, 0.7-1.0X as long as hind coxa; petiole smooth with irregular longitudinal rugae, the basal flange prominent or weak. First valvula of ovipositor with lateral line of 7 to 8 prominent teeth; second valvula broad with 9 lateral teeth connected dorsally by weak transverse ridges.

Description of male.—Length, 2.6-3.1 mm. Eyes separated by 1.7-1.9X their height. Malar space 0.7-0.9X height of eye. Flagellum (Fig. 7) slightly longer than in female, 2.0-2.2X height of head. Fore wing 2.0-2.4X as long as broad. Petiole 3.1-3.4X as long as broad, 1.2-1.5X as long as hind coxa.

Distribution (see Fig. 7, Heraty in press-b).—Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Uruguay.

Variation.—Minor differences occur in the shape of the body. Specimens from northern Brazil and Ecuador have a generally less robust mesosoma, and the axillula is more distinctly flattened than from southern South America. Fore wings vary in length of the marginal fringe, pilosity of the cubital vein and number of setae surrounding the base of the speculum. Over the range of this species, the anellus may be yellow or brown, but the scape is always a distinct yellow or orangish yellow. The degree of infuscation of the femora of females can vary from only a faint infuscation to an almost complete darkening. Males may have either yellow or infuscate femora, which is typical of other species of *Oreasema* in which females have dark femora. The holotype male of *O. paraguayensis* belongs to a dark colored population found in the western Argentinian states of Jujuy, La Rioja and Salta. Individuals of this dark form have the head and mesosoma almost black, and the hind femora of both males and females are dark brown with red-

dish reflections. The variation over the vast range of this species may result from differences in either habitat or host.

Remarks.—Specimens that were referred to as "*Oreasema* sp." in papers by Wojcik (1988, 1989, 1990), Wojcik et al. (1987) and Vander Meer et al. (1989) were examined and belong to this species. A single specimen from the Mato Grosso Province in Brazil (Docias [?], iv.1972, ex *Solenopsis* nest, USNM) also belongs to this species, and I assume this is part of the material referred to in Williams and Whitcomb (1973) and Williams (1980). Silveira-Guido et al. (1964) refers to "adults" that were reared from *S. richteri* and identified as *O. doellojuradoi* by Burks (USNM). Silveira-Guido et al. (1964) state that these were subsequently used by De Santis for his description of *O. crassa*. De Santis (1968) makes no reference to the host of this species, nor to Burks' identification, and only the holotype is known from the type locality. Siviera-Guido et al. (1964) refer to other localities in Uruguay (Colonia San Gregorio and Arroceria San Pedro), but I have not been able to examine these specimens. Habitus drawings in Silveira-Guido et al. (1964) appear to be *O. xanthopus* (although with an elongate petiole as in *O. pireta*).

Host Ant.—*Solenopsis invicta* and *Solenopsis* sp. *saevissima*-complex (Myrmicinae) (De Santis 1968; Williams and Whitcomb 1973; Wojcik 1988, 1989, 1990; Wojcik et al. 1987; Vander Meer et al. 1987), and possibly *S. richteri* (Silveira-Guido et al. 1964). The range of *O. xanthopus* is similar to that of the *Solenopsis saevissima*-complex in South America, as illustrated in Wilson (1952). Trager (1991) distinguished 11 species of the *Solenopsis saevissima*-complex that occupy various regions of this same range. The distribution of *O. xanthopus* suggests that it may parasitize more than just the two presently known species.

Host Plant.—Unknown. Males have been collected resting on grasses and a variety of broad-leaf plants over fire ant nests [a variety of grasses, annuals, herbs, legumes, shrubs, and trees were examined for evidence of egg laying and planidia without success].

Habitat.—Disturbed Cerrado, pantanal, and Campo Limpo. Most of the fire ant colonies collected in the 1984-86 survey were found along road

shoulders where fire ants flourish. The soils along the roads varied considerably. Fire ant colonies were generally collected in disturbed habitats.

Immature stages.

Eggs (dissected from abdomen).—Stalked eggs as typical of other *Orasema*.

First-instar larva (Figs. 11-13, 15, 16).—Larval form typical for *Orasema* and recognized by the following features: three pairs of cranial sensillae, cranial spines absent; terga IV-VI acuminate laterally, terga VII-VIII strongly scalloped ventrally; caudal cerci short; desclerotized lines from base of setae prominent. Average length of unfed larva 0.21 mm (SD= 0.02, n = 5), maximum size of distended first instar (Fig. 16) 1.20 mm (n=1).

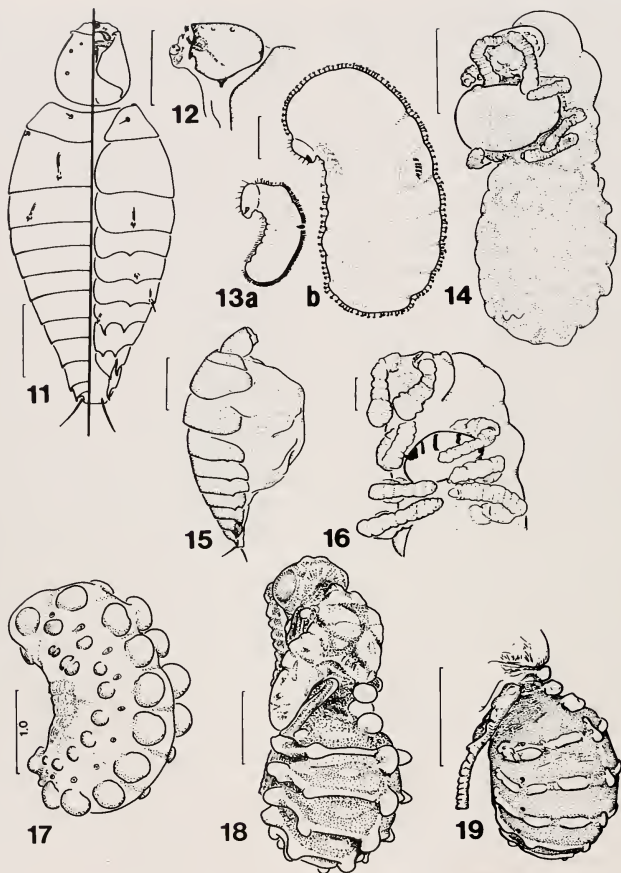
Second-instar larva (Fig. 14).—Recognized by the following characters: body white and unsclerotized; mandibles lacking; only a single mesothoracic spiracle anteroventral of first tubercle; only nine dorsal tubercles present, tubercles slightly raised. Length 1.26 mm (n=1).

Third-instar larva (Fig. 17).—Mature larvae recognized by: body white and poorly sclerotized, dorsal surface smooth; oral region with circular region of fine striae convergent to midline, mandibles lacking; two thoracic and seven abdominal spiracles present on raised tubercles on body segments II-X; body segments II-X with nine enlarged dorsolateral tubercles, segments I-X with series of ten smaller lateral tubercles; segments II and III with pair of medially divided tubercles lateral to oral region. Average length of pupa 2.81 mm (SD=0.13, n=10). Prepupa recognized by definition of antennal segments on ventrolateral margins of abdominal segments and by tubercles more prominent.

Pupa (Fig. 8).—Pupal form is typical for other species of *Orasema* and is recognized by: three enlarged tubercles over petiole; five transverse abdominal ridges with prominent tubercles dorsally (much larger than for other species), laterally and subventrally. Average length 3.43 mm (SD=0.21, n=10).

Material Examined.—[in following list, ?=adult with sex undetermined; L=larvae; P=pupae; PH=phthysergate] ARGENTINA: *Jujuy*: Palpala, i (1?, NMBA); *La Rioja*: February (1 female, NMBA); *Salta*: (1 male, NMBA); *Cachi*, i (1 fe-

male, MLTA); *Santiago del Estero*: i (1 female, MCZ). BOLIVIA: *Santa Cruz*: San Matias, iii, ex floated *S. invicta* [colony] 86-131 (6P); 5 km E of San Matias, iii, ex floated *S. invicta* 86-136 (1L, 9P) & 86-137 (3?, 1L, 9P); Las Juntas, xii (2 females, CARN). BRAZIL: *Amazonas*: Manaus (1 female, USNM); Fonte Boa, ix (14 females, CNC); *Goiás*: Jataí, xi (1 female, CNC); *Mato Grosso*: Cáceres, ex *S. invicta* 86-49 & 86-102 (5 females, 2 males, 6L, 9P, JMH); Cáceres, viii, ex *S. invicta* 85-450 (15 females, 31P, JMH); Cáceres, viii, 85-388, ex *S. invicta* (15 females, 4 males, 6P, JMH, NMBA); Docias[?], iv, *Solenopsis* nest (1 female, USNM); Fazenda Paiól, BR-070, km 677, 50 km E of Cáceres, vii, ex floated *S. invicta* 85-388 (13?, 3L, 35P, 7PH, FLA); Fazenda Sta. Isabel, Reserve do IBDF, MT-060, km 118 (Transpantaneira), xii, ex floated *S. invicta* 84-306 (4?, 6P, FLA); Fazenda SATO, BR-070, km 708, 19 km E of Cáceres, xi, ex floated *S. invicta* 86-570 (7?, 23L, 135P, 1PH, FLA); Fazenda SATO, BR-070, km 708, 19 km E of Cáceres, xi, ex floated *S. invicta* 86-571 (2?, 33L, 157P, 1PH skin with large larva attached, JMH); Porto Jofre, xii, ex floated *S. invicta* 84-296 (1?, FLA); Quatro Marcos, Fazenda Bela Vista, iv, ex floated *S. invicta* 85-B-164 (3?, 3L, 20P, 1PH, FLA); Sete porcos, BR-070, km 616, (100 km W of Cuiabá), viii, ex floated *S. invicta* 86-B-451 (2?, 1L, 8P, FLA); Jacobina, BR-070, km 701, 26 km E of Cáceres, viii, ex floated *S. invicta* 85-421 (5?, 17P, FLA); Jacobina, BR-070, km 701, Jacobina, 26 km E of Cáceres, viii, ex floated *S. invicta* 85-422 (5?, 13P, FLA); *Mato Grosso do Sul*: Corumba (1 female, USNM); MS-80, 48 km NW of Campo Grande, ii, ex floated *S. invicta* 86-B-49 (19?, 67L, 412P, 46PH, JMH) & also 2 males flying over same colony; same locality, iii, 86-B-64 (23?, 5L, 312P, 13PH, JMH); same locality, iii, 86-B-65 (59?, 53L, 444P, 21PH, FLA, NMBA) & 10 flying over same colony; same locality, vi, 86-320 (4?, 7L, 19P, 1PH skin, FLA); Rochedo, iii, ex floated *S. invicta* 86-B-102 (2P, FLA); Jacobina, BR-70, km 32, viii, 85-422 & 85-421, ex *S. invicta* (4 females, 5 males, JMH); *Para*: Belm, vii (1 male, USNM); Jacareacanga, xii (5 females, AEI); Santarem (1 female, CARN); Santarem (3 females, USNM). COLOMBIA: *Amazonas*: Leticia, ii, MT (4 females, CNC). EC-UADOR: *Napo*: Cocoa River, iv (2 females, CNC);



Figs. 11-19. 11-18. Immature stages of *Orasema xanthopus*. 11, unfed first-instar, dorsal (left) and ventral (right) view. 12, head of unfed first instar in lateral view. 13, first instar larva: a, external position of first instar (arrow) on second-instar larva of *Solenopsis invicta*; b, partially fed first instar beneath cuticle of fourth-instar larva of *Solenopsis*. 14, second instar feeding on host pupa. 15, partially fed first instar removed from host larva. 16, first instar feeding in external position on host pupa. 17, mature third instar in lateral view. 18, pupa in dorsolateral view. 19, *O. salebrosa*, metasoma of female pupa. Scale bars represent mm in following scales: 11, 12 = 0.04; 13, 16 = 0.5; 15 = 0.05; 14, 17-19 = 1.0.

Tena, ii (5 females, CNC); Tena, ii (2 females, CNC); Tena, ii (2 females, CNC); Puerto Misahuali, 350m, ii (1 female, CNC); Limoncocha, ii (4 females, CNC); Limoncocha on Rio Napo, i-iii MT (8 females, FLA). GUYANA: Georgetown, vi (1 female, UMS). PERU: Loreto: Dept. Loreto Explorama Inn, 40 km NE Inquitos on Amazon R., vii (1 female, CNC); Madre de Dios: Avispas, 400m, ix, (4 females, CNC). URUGUAY: Artigas, iii, fire ant project (2 females, USNM).

Behaviour of O. xanthopus.—Observations on *O. xanthopus* parasitizing *S. invicta* were made as part of a survey to evaluate the natural biological control agents of fire ants in Mato Grosso (MT) and Mato Grosso do Sul (MS), Brazil. The survey was conducted by flotation examination of standardized fire ant nest samples of 2-1/2 liters of tumulus (Wojcik 1988). From June 1984 through December 1986, 1585 fire ant colonies were sampled. Most colonies were collected within 150 km of Cáceres (MT); some samples were collected near Cuiabá and along the Transpantaneira highway from Poconé to Porto Jofre (MT), 228 colonies from within 200 km of Campo Grande (MS), and 16 colonies from western Bolivia.

Orasema xanthopus occurred in 33.2% of the collections from *Solenopsis* nests made in the Central-West region of Brazil, and was the most commonly collected myrmecophile in *S. invicta* (=saevissima-complex) nests (Wojcik 1988). The average number of parasites collected was 18.3 per nest, although one colony contained 598 *O. xanthopus* larvae, pupae, and adults. Larval counts do not include first-instar larvae and parasitism rates are higher than was first recorded. Monthly collection data show a consistent presence of all life stages with *O. xanthopus* present in 18.5-67.5% of colonies examined throughout the year (Table 1).

Aspects of biology for this species, studied in laboratory fire ant nests, are similar to other *Orasema* species (Wheeler 1907, Johnson et al. 1986). The particular plants utilized by this species for oviposition were not determined. First-instar larvae were found on the external surface of second-instar ant larvae or just under the cuticle of mature ant larvae (Figs. 8, 9), entering the host at various locations on the dorsal region of the thorax and abdomen. Only one endoparasitic first-instar larva was observed

per host larva or pupa. Partial endoparasitic feeding, as evidenced by distention of the first-instar larva (Fig. 11), took place only after the parasite burrowed into the host (Fig. 9). After host pupation, the now ectoparasitic first and later instars feed on the ventral region of the thorax, between the deformed pupal legs of the host (Fig. 12). Mature larvae detach themselves from the host after feeding is completed. The host may or may not be entirely consumed, we have 3 examples of large *O. xanthopus* larvae with their heads (mouthparts) still inserted in the cuticular skins of completely or mostly consumed ant pupae. Deformed host pupae, resulting from incomplete feeding, remain alive within the nest and are here referred to only as phthisergates (after Wheeler 1907). Phthisergates may live for some time in the colonies, but never develop into adult ants. Their presence is diagnostic of parasitism by *Orasema*.

During the pupal period, parasite pupae are mixed in with host brood, and are cared for like ant pupae (Silveira Guido et al. 1964, Williams 1980, Wojcik 1990). Worker ants assist eclosion by the parasite pupae in the same manner as the ants assist their own pupae (Silveira Guido et al. 1964, Wojcik 1990). Fed and groomed by the worker ants, adult parasites are temporarily integrated into the colony (Silveira Guido et al. 1964, Williams 1980, Wojcik 1990). When a nest is disturbed, the pupal and adult parasites are rescued by the ants seemingly in preference to their own brood (Wojcik 1990). Several ants in the alcohol samples were found clutching the dorsal nodes of larvae and pupae.

The manner in which adults of *O. xanthopus* leave the nest has not been observed. Males hover over the ant nest, or rest on grasses and other plants around and over the fire ant nests (Williams 1980, Wojcik & Jouvenaz unpublished). Mating swarms, with males flying in a low swarm over the fire ant mound, were observed over a three-day period at one site in Mato Grosso do Sul (MS-80) in March, 1986. Case 1: colony 86-B-49, 4 days after being disturbed by digging; flight activity was high when observations started at 8:45 AM, with activity subsiding by 9:15 A.M., but continuing until 9:34 A.M. with an increase in winds and temperature, none of the other 15 other mounds within 100 m showed any flight activity of *Orasema*. Case 2: colonies 86-

Table 1. Summary of collections of *Orasema xanthopus* floated from South American fire ant colonies, June 1984 to December 1986. Counts do not include first-instar larvae.

Month	Colonies examined	Colonies w/ <i>Orasema</i>	%	# of larvae	Colonies w/larvae	# of pupae	Colonies w/pupae	# of adults	Colonies w/adults	Total <i>Orasema</i>	Mean	Range
Jan	86	30	34.9	146	14	230	28	48	21	424	14.1	1-123
Feb	115	65	56.6	305	26	1451	62	230	34	1985	30.5	1-598
March	106	33	31.1	107	20	894	24	97	11	1098	33.3	1-556
April	40	27	67.5	86	15	304	27	43	10	433	16.0	1-165
May	189	51	27.0	85	15	456	46	109	29	650	12.8	1-154
June	164	41	25.0	367	19	845	36	84	13	1296	31.6	1-446
July	132	54	40.9	93	12	416	46	171	39	680	12.6	1-74
Aug	225	79	35.1	85	24	924	70	255	46	1264	16.0	1-203
Sept	142	42	29.6	15	4	222	35	84	20	321	7.6	1-59
Oct	146	27	18.5	23	13	160	22	25	12	208	7.7	1-60
Nov	171	62	36.3	215	25	874	55	75	24	1164	18.8	1-192
Dec	69	15	21.7	6	4	63	12	31	11	100	6.7	1-29
Totals	1585	526	33.2	1533	191	6839	463	1252	270	9623	18.3	1-598

B-64 & 86-B-65, 3 days after being disturbed by digging. 86-B-65 moved 1 m NW; flight activity was observed at 11 AM after sun appeared from clouds (heavy overcast until then); winds calm. Case 3: colonies 86-B-64 & 86-B-65, 4 days after being disturbed by digging; flight activity was high when observations started at 9:11 AM, light overcast till 10:25 then full sun, sporadic flying with full sun for 1/2 hr before wasps ceased to fly, one of the other 6 mounds within 100 m had flight activity; winds calm. Wojcik observed several males that approached and attempted to mount other resting males on grass leaves or stems over the ant mound at the edges of the swarm. The standing males repelled the apparently misguided males by wing flipping, by antennal fencing, or by leaving the area.

Mating takes place immediately after adult parasites leave the nest (Williams 1980). Based on the relatively even distribution of the larvae, pupae, and adults collected (Table 1), it seems likely that overlapping multiple generations occur in Central-West Brazil and mating takes place whenever weather conditions are suitable. No fire ant mating flights occurred during the wasp mating swarms (from any colonies within walking distance) and no unusual fire ant activity was observed on any of the studied mounds.

Studies of cuticular hydrocarbons have shown that *O. xanthopus* larvae, pupae and adults possess only host *Solenopsis* sp. cuticular hydrocarbons while in the ant nest. After leaving the host nest, adult *O. xanthopus* acquire species-specific cuticular hydrocarbons and lose the majority of the host *Solenopsis* sp. cuticular hydrocarbons (Vander Meer et al. 1989).

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**Nesting Biology of *Microstigmus myersi* Turner,
a Wasp With Long-haired Larvae (Hymenoptera: Sphecidae, Pemphredoninae)**

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Abstract.—This paper describes the nesting habits of *Microstigmus myersi*, a species which builds nests with dirt particles hanging on fine roots in banks. The nest has no petiole and rests directly on the end of a rootlet. The entrance is shaped like a tube and is located in the lower part, whereas the cells are located above, forming the upper part of the nest. This species performs semiprogressive provisioning and preys on Thysanoptera nymphs. *Microstigmus myersi* larvae have long hairs on their body. Considering the orientation of the brood cells of this species, the larval hairs seem to represent an adaptation that may permit better support within the cells. The larvae have spinnerets and spin a cocoon, in contrast to what occurs in most other *Microstigmus* species. The nests of *M. myersi* are parasitized by *Heterospilus* sp. (Braconidae), and also by *Ceraphron* sp. (Hymenoptera, Ceraphronidae). The large number of cells in some of the nests seems to indicate long duration of these nests and, indirectly, the possibility of reuse by descendants. The nests normally contain more than one female and some males.

The genus *Microstigmus* Ducke is a highly interesting group within the Sphecidae, especially because of its nests and the social behavior exhibited by some of its species (Matthews 1968a, 1968b, 1991; Richards 1972; West-Eberhard 1977; Ross and Matthews 1989a). In general the nests are small sacs built with particulate material aggregated with silk produced by females (Matthews 1968b; West-Eberhard 1977; Matthews and Starr 1984). In most species these sacs hang on a fine petiole (West-Eberhard 1977).

Although *Microstigmus* is widely distributed in the Neotropical region, little is known about its biology. Only *M. comes* Krombein, a species found in Costa Rica, has been studied in some depth. This species nests under the leaves of palms of the genus *Cryosophylla* Blume and builds spherical nests using material scraped off the bottom surface of the leaves (Matthews 1968b; Matthews and Starr 1984). Ross and Matthews (1989a, 1989b) have presented evidence that most of the colonies may be eusocial, with task division among females based on size.

Some aspects of the nesting biology of *M. myersi* Turner were first reported by Myers (1934). Myers did not provide a very detailed report on the biology of *M. myersi* but stated that the nest is quite similar to that of *M. theridii* Ducke in general appearance,

size and structure. The nest found by him was suspended by a long fine rootlet, under a bank, and had numerous earth pellets incorporated in the walls.

The present paper reports on aspects of the nesting habits of *M. myersi*. The descriptions are based on ten nests collected on the campus of the Federal University of Viçosa (MG), Brazil, from April 1989 to January 1992. Nest structure and cell contents were examined under a stereoscopic microscope. Observations made directly at the nesting sites on other nests that were not collected are also reported. The species was identified by the first author. Voucher specimens are deposited in the Entomological Museum of the Federal University of Viçosa and in the Museu de Zoologia da Universidade de São Paulo (MZSP).

NESTING SITE AND NEST ARCHITECTURE

Nests of *M. myersi* were found only on steep banks mainly along roads and paths inside or close to wooded areas. As described by Myers (1934), the nests hang from fine rootlets. In general they are inconspicuous because of their similarity to the numerous dirt clumps also hanging from fine roots (Fig. 1). The schematic drawing presented in Fig. 1 is typical of the banks used by *M. myersi* (presence

of an upturned edge in the upper part containing many root ends). Normally the nests are not clustered, although as many as four nests were found close to one another in the same bank.

The nest architecture is quite different from that found in other *Microstigmus* species whose nest architecture is known. The nest has no petiole and

rests directly on the end of a rootlet. The entrance is shaped like a tube and is located in the lower part, whereas the cells are located above, forming the upper part of the nest (Fig. 2). In new nests, all cells are vertically oriented with their opening looking down (Fig. 3b). As the nest grows, additional cells are oriented obliquely (Fig. 3a).



Fig. 1. Cross-section of a typical bank used as nesting site by *Microstigmus myersi*. Only one nest is represented in the sketch.



Fig. 2. Nest of *Microstigmus myersi*. Note the silk around the supporting rootlet on the upper part of the nest. Scale line = 5mm.

The walls of the nest are built with dirt particles aggregated with silk produced by females. Internally, the nest is fully lined with silk. The region of transition between the supporting root and the nest wall on the upper part is covered with a lot of silk, which gives it a whitish color. In general, the nests are built at the end of the rootlets, so that the rootlet tip is always inside the nest. However, in some nests the root extends beyond the nest (Fig. 3b).

In most of the nests found, the outlines of the cells can be discerned on the outer surface of the nest (Fig. 2), although one nest had a spherical outer contour (Fig. 3a). This latter nest was covered with a weak layer of dirt particles and, judging from the number of cells (23), appeared to be quite old. Observations revealed that these particles are gradually brought by females and attached to the outer part of the nest with silk. The females climb up the supporting root to the region where the root penetrates the bank and bring back dirt particles holding them between their mandibles. It seems that all nests tend to develop a smoother outer surface as they get older.

West-Eberhard (1977, Fig. 2B) has presented a schematic drawing of a nest with architecture similar to that of *M. myersi*. The author refers to this nest as belonging to a new well-distinct species. It is possible that this species belongs to the same group as *M. myersi*.

The differences between the nests of *M. myersi* found at Viçosa and that described by Myers may

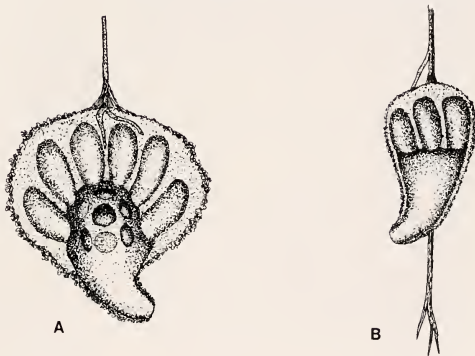


Fig. 3. Cross-section of *Microstigmus myersi* nests: a - old nest; b - newly founded nest.

be due to an error he made in describing the orientation of the nest. On the other hand, the material found in Viçosa may belong to another species closely related to *M. myersi*.

NEST CONTENTS AND IMMATURES

Table 1 summarizes the contents of the nests. The cells of *M. myersi* are provisioned with Thysanoptera nymphs and not with Collembola, as suggested by the title of the study by Myers (1934). *Microstigmus myersi* performs semi-progressive provisioning since cells with eggs contained only 3 to 15 Thysanoptera nymphs. Furthermore, the nymphs are placed loose within the cell and do not form a compact mass as observed in species performing mass provisioning. The number of prey in cells with immature larvae was similar to that found in cells with eggs, excepting some immature larvae that were found in cells that did not contain food provisions. As in other *Microstigmus* species, the preys are supported in the cells by silk threads.

Contrary to what is observed for most Apocrita, *M. myersi* larvae have long hairs on their body. In 1st- and 2nd-instar larvae, the hairs are short (Fig. 4b), whereas in older larvae they are longer and curved at the end (Fig. 4a). Among Sphecidae, hairy larvae are encountered only in a few genera not related to *Microstigmus* (Evans 1959).

Considering the orientation of the brood cells of this species, the hairs of *M. myersi* larvae seem to represent an adaptation that may permit better support within the cells. These hairs may attach to the silk threads placed by female on the cell bottom to support eggs and prey, thus permitting the larva to stay suspended within the cell. There are evidences that the nest architecture of *M. myersi* evolved independently from that found in the species with pendulous nests and with glabrous larvae (Melo, in prep.).

Lanham (1979) stated that the larval hairs found in ants and allodapine bees probably represent an adaptation for life in a communal brood chamber. Lanham (1980), in a discussion on the origin of

Table 1. Contents of *Microstigmus myersi* nests collected in Viçosa (MG), Brazil.

NEST NUMBER	ADULTS		NUMBER OF CELLS	EMPTY CELLS	PREYS ^a ONLY	EGG	LARVA	PREPUPA	PUPA		PARASITES
	F	M							F	M	
—	-	-	23	14	0	03	02	02	2	0	0
—	1	0	03	01	0	02	0	0	0	0	0
A	5	3	12	01	01	01	01	04	4	0	0
B	1	2	07	02	0	02	02	0	1	0	0
296	2	1	08	0	01	0	02	03	1	1	0 _b
328	2	0	18	05	01	01	03	03	3	1	01 ^c
376	3	1	09	01	03	01	01	0	2	0	01 ^c
584	2	1	08	0	01	01	01	0	2	2	0 _b
586	4	2	13	05	01	02	0	0	2	0	03 _b
589	1	0	07	0	01	02	02	02	0	0	0

a. Although *Microstigmus myersi* exhibits semi-progressive provisioning, the number of cells that possess only thrips nymphs is also indicated.

b. *Heterospilus*.

c. *Ceraphron*.

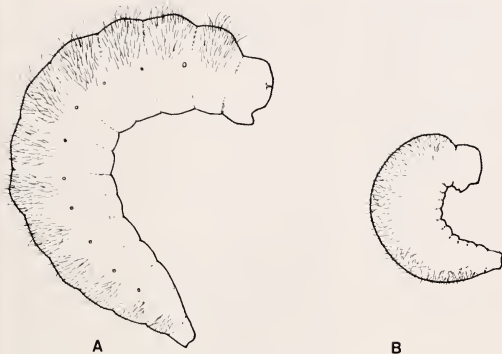


Fig. 4. Larvae of *Microstigmus myersi*: a - predefecating larva; b - young larva. Scale line = 1mm.

bees, hypothesizes that in the yet unstudied species of *Microstigmus* there may be found an evolutionary sequence in which cell making is abandoned and the larvae have become hairy. As previously mentioned, although *M. myersi* has hairy larvae, the immatures of this species are reared in individual cells. In all *Microstigmus* species whose nest architecture is known, the immatures are reared in individual cells.

Microstigmus myersi larvae have spinnerets and spin a cocoon, in contrast to what occurs in most other *Microstigmus* species (Melo, in prep.). After cocoon spinning, the larvae orient with their head facing outward and their anal end facing the vestibule. All prepupae and pupae were found within a cocoon and facing outward. The adults make holes in the cocoon in the region of cell opening and remove the larval feces. The feces stick to the inner wall of the cocoon and are not always fully removed by the adults. This cleaning behavior by the adults was inferred from the observation of the cap of cells containing predefecating larvae, prepupae and pupae. The cells are probably cleaned completely only after imago emergence.

PARASITOIDS

The nests of *M. myersi* are parasitized by a species of *Heterospilus* Haliday differing from *H. microstigma* Richards (Braconidae). *Heterospilus*

microstigma is testaceous in color and its larvae spin a thin cocoon, while this other species has a black body and its larvae spin a very rigid cocoon.

The imagoes of this *Heterospilus* species emerge from the cell through a hole in the cocoon which they make at the end facing the outer side of the nest. It is common to find cells which have been opened outward and are closed inside and which are lined with a rigid cocoon, indicating an emergence by the parasitoid.

Microstigmus myersi adults apparently are unable to open these cocoons, so that parasitized cells become useless. In some older nests, the entire upper part of the nest can be formed by this type of cell. In general, the opening made in the cocoon by the parasitoid is closed by the wasps with silk and dirt particles.

In one nest (N376), we also found a cell parasitized by a species of *Ceraphron* Jurine (Ceraphronidae), in which five larvae were eating a prepupa.

SOCIAL ORGANIZATION

Little can be inferred about the social organization of *M. myersi* from the present data. The large number of cells in some of the nests seems to indicate long duration of these nests and, indirectly, the possibility of reuse by descendants. Cell reuse was also inferred by the presence of eggs or

immature larvae in cells lined with cocoons. The nests normally present more than one female and some males (Table 1). The relationship between number of cells with eggs and larvae and number of females does not permit us to draw conclusions about the occurrence of dominance among females. Although no quantitative analysis was performed, nest-sharing females do not exhibit marked differences in size.

Adults walking over the nest are commonly observed, a behavior which appears to be related to defense against parasitoids, as also observed by Matthews (1968b) in *M. comes*. Since the males of *M. myersi* are not easily distinguished from females in field conditions, we do not know if the males also exhibit this behavior.

ACKNOWLEDGMENTS

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Sawflies of the Genus *Perineura* Hartig from Japan (Hymenoptera: Tenthredinidae)

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Abstract.— Two new species of *Perineura* from Japan are described and illustrated, *P. kamikochiana*, sp. nov., and *P. nigra*, sp. nov. A key and illustrations are provided for separation of the Japanese species of *Perineura*.

Perineura is a small genus in the subfamily Tenthredininae. It was represented by six species in Europe and Japan. In Japan, five species, *P. esakii* Takeuchi, *P. pictipennis* Takeuchi, *P. japonica* Malaise, *P. stigma* Takeuchi, and *P. okutanii* Takeuchi, were recorded. Recently, I had an opportunity to examine 27 specimens of *Perineura* collected in Japan. They represent seven species, including two new species, *P. nigra* and *P. kamikochiana*, which are described below. Although Benson (1952) stated that the male of the European species, *Perineura rubi* (Panzer), is far more commonly found than the female, most of the specimens I have from Japan are females, and the males are not known or have not been associated with females. Also, the Japanese species described by Takeuchi (1959) and Malaise (1931) are based on females. Consequently, this review is based on females. Host plants of the species in Japan are unknown.

Perineura Hartig

Perineura Hartig, 1837: 303. Type species: *Tenthredo rubi* Panzer, by monotypy.
Synaurema Hartig, 1837: 314. Type species: *Tenthredo delicatula* Klug (= *Perineura rubi* Panzer), by monotypy.

Diagnosis.— Clypeus with anterior margin deeply and subtriangularly emarginate; malar space broad, nearly 2X diameter of front ocellus; occipital carina well defined on entire occipital margin; antenna fairly long, 2X or more head width and filiform, 3rd and 4th segments nearly equal in length; anal cell of forewing with 2A+3A meeting 1A or with a short straight anal crossvein at about basal third; hindwing with two middle cells in female and a marginal vein in male; first abdominal tergum divided; tarsal claw with short inner tooth, much smaller than outer tooth.

KEY TO FEMALES OF THE JAPANESE SPECIES OF *PERINEURA*

1. Antenna black (Fig. 9); forewing without a dark band below stigma (Figs. 12, 14-16) or with a small pale fleck below stigma (Fig. 13); *japonica* group 3
- Antenna with three apical segments white (Fig. 8); forewing with a dark band below stigma (Figs. 10, 11); *esakii* group 2
2. Tegula black, scutellum and posttergite nearly white; lancet with 20 serrulae, with basal 3 serrulae as in Fig. 31 *esakii* Takeuchi
- Tegula white, scutellum and posttergite nearly black; lancet with 19 serrulae, with basal 3 serrulae as in Fig. 32 *pictipennis* Takeuchi
3. Abdomen nearly fulvous (Figs. 26-28) 4
- Abdomen black (Fig. 30), or 2nd to 7th abdominal tergites with yellow fleck (Fig. 29) 6
4. Forewing with a pale brown fleck below stigma (Fig. 13); color pattern of abdomen as in Fig. 27; sawsheath as in Fig. 22; lancet with 19 serrulae, with basal 3 serrulae as in Fig. 34 *stigma* Takeuchi

- Forewing without a pale brown fleck below stigma (Figs. 12, 14-16); other features various5
- 5. Stigma of forewing nearly uniformly pale reddish yellow (Fig. 12); mesonotum with some yellow flecks (Fig. 17); color pattern of abdomen as in Fig. 26; sawsheath as in Fig. 21; lancet with 19 serrulae, with basal 3 serrulae as in Fig. 33*japonica* Malaise
- Stigma of forewing dark brown with basal third white (Fig. 14); mesonotum black; color pattern of abdomen as in Fig. 28; sawsheath as in Fig. 23; lancet with 19 serrulae, with basal 3 serrulae as in Fig. 35*okutanii* Takeuchi
- 6. Abdomen black; mesonotum and mesepisternum black; sawsheath as in Fig. 25; lancet with 20 serrulae, basal 3 serrulae as in Fig. 37*nigra*, sp. nov.
- Abdomen black with yellow fleck on 2nd to 7th tergites (Fig. 29); mesonotum with a V-like fleck (Fig. 18) and mesepisternum with a yellow fleck; sawsheath as in Fig. 24; lancet with 19 serrulae, with basal 3 serrulae as in Fig. 36*kamikochiana*, sp. nov.

***Perineura kamikochiana* Togashi, sp. nov.**

Female.— Length, 8.0 mm. Body black with following parts pale yellow to yellow: upper half of inner and hind orbits (Fig. 6), anterior half of clypeus, labrum, basal half of mandible, maxillary and labial palpi, tegula, pronotum, V-like fleck on mesonotum (Fig. 18), mesoscutellum except for posterior third, posttergite, most of metascutellum, central portion of metanotum, fleck on mesepisternum, triangular-like fleck on 2nd to 7th tergites, 8th and 9th tergites except for black lateral sides (Fig. 29), cercus, and 7th and 8th abdominal sternites. Antenna black. Wings rather yellowish hyaline, stigma of forewing pale yellow but apical third dark brown (Fig. 15), costa of forewing dark brown, other veins black. Legs yellow, fore and mid tibiae pale to dark brown, apical portion of hind femur with small dark brown spot.

Head: Postocellar area rather flat; postocellar furrow nearly absent; lateral furrow deep (Fig. 6); interocellar furrow distinct but shallow; OOL:POL:OCL = 2.5:1.0:1.0; frontal area slightly concave and connected with median fovea; lateral fovea linear; ratio between antenno-ocular distance and distance between antennal sockets about 1.0:0.85; supraclypeal area slightly convex; clypeus nearly flattened; postorbital groove distinct. Antenna slightly longer than costa of forewing (ratio about 1.0:0.9), relative length of segments about 1.4:1.0:4.1:3.5:3.2:2.5:2.2:2.0:2.1.

Thorax: Normal; wing venation as in Fig. 15; hind basitarsus shorter than following 4 segments combined (ratio about 1.0:1.3).

Abdomen: Normal; sawsheath as in Fig. 24; lancet with 19 serrulae, basal 3 serrulae as in Fig. 36.

Punctuation: Head covered with fine setigerous punctures but supraclypeal area nearly impunctate, shining; basal half of clypeus sparsely and finely punctured; cheek covered with medium sized punctures. Pronotum, praescutum, and thorax ventrally covered with fine setigerous punctures; mesonotal lateral lobes, sunken areas, mesoscutellum except for posterior 1/4, and posttergite nearly impunctate, shining; posterior 1/4 of mesoscutellum distinctly and evenly punctured, but posterior margin rugosoreticulately sculptured. Abdominal tergites shagreened.

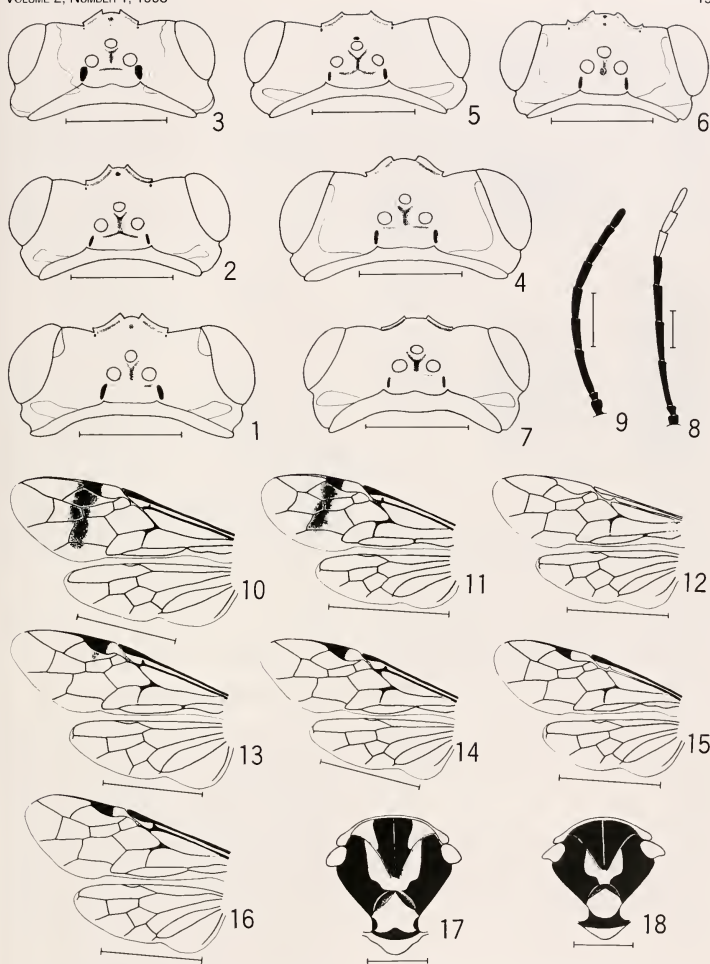
Distribution.— Japan (Honshu).

Holotype.— Female, 21-23.VI.1989, Kamikochi (altitude 1500 m), Nagano Prefecture, A. Shinohara leg. Deposited in the National Science Museum (Natural History), Tokyo.

Remarks.— This new species resembles species assigned to the *japonica* group, but is distinguished from them by the mostly black abdomen (species of the *japonica* group have the abdomen mostly fulvous, see Figs. 26-28).

***Perineura nigra* Togashi, sp. nov.**

Female.— Length, 8.5 mm. Body black with following parts pale yellow to yellow: anterior half of clypeus, labrum, maxillary and labial palpi, fleck on postorbit (Fig. 7), posterior margin of pronotum, tegula, cenchrus, posterior margin of 1st abdominal tergite (Fig. 30), 9th tergite, and cercus. Antenna black. Wings slightly smoky, hyaline, stigma of



Figs. 1-18. 1-7, Head, dorsal view. 1, *Perineura esakii*. 2, *P. pictipennis*. 3, *P. japonica*. 4, *P. stigma*. 5, *P. okutanii*. 6, *P. kamikochiana*. 7, *P. nigra*. 8-9, Antenna, lateral view. 8, *P. esakii*. 9, *P. okutanii*. 10-16, Wing venation. 10, *P. esakii*. 11, *P. pictipennis*. 12, *P. japonica*. 13, *P. stigma*. 14, *P. okutanii*. 15, *P. kamikochiana*. 16, *P. nigra*. 17-18, Thorax, dorsal view. 17, *P. japonica*. 18, *P. kamikochiana*. (Scale of 1-9 and 17-18, 1.0 mm; 10-16, 5.0 mm.)

forewing except for basal 1/4 and other veins dark brown to black, basal 1/4 of stigma pale yellow (Fig. 16). Legs fulvous, but all coxae black, apical portion of all tarsi become darker.

Head: Postocellar area nearly flattened; postocellar furrow ill-defined; lateral furrow distinct (Fig. 7); interocellar furrow slightly depressed; frontal area nearly flattened; median fovea shallow, circular in outline; lateral fovea deep; ratio between antenno-ocular distance and distance between antennal sockets about 1.5:1.0; supraclypeal area nearly flat; clypeus nearly flat; labrum nearly flat; postorbital groove distinct. Antenna shorter than costa of forewing (ratio about 1.0:1.1), relative length of segments about 1.6:1.0:3.6:3.0:2.9:2.4:1.8:1.8:2.0.

Thorax: Normal; mesoscutellum slightly convex; wing venation as in Fig. 16; hind basitarsus slightly shorter than following 3 segments combined (ratio about 1.0:1.1).

Abdomen: Normal; sawsheath as in Fig. 25; lancet with 20 serrulae, basal 3 serrulae as in Fig. 37.

Punctuation: Head covered with fine setigerous punctures; supraclypeal area nearly impunctate, shining; pronotum, praescutum, and thorax ventrally covered with fine setigerous punctures; mesonotal lateral lobes, sunken areas, mesoscutellum except for posterior 1/4, metascutellum, and metanotum nearly impunctate, shining; posterior 1/4 of mesoscutellum distinctly and evenly punctured; abdominal tergites shagreened.

Distribution.— Japan (Honshu).

Holotype.— Female, 4.V.1974, Mt. Jinba, Tokyo Metropolitan, A. Shinohara leg. Deposited in the National Science Museum (Natural History), Tokyo.

Remarks.— This new species closely resembles *P. kamikochiana*, but it is distinguished from the latter by the black mesonotum and abdomen (in *P. kamikochiana* the mesonotum and abdomen have yellow flecks, see Figs. 18, 29), and by the 20 serrulae and the shape of the basal three serrulae of the lancet (in *P. kamikochiana* the lancet has 19 serrulae and the basal 3 serrulae have two subbasal teeth, see Fig. 36).

Perineura esakii Takeuchi

Perineura esakii Takeuchi, 1959: 70.

Specimen examined.— One female, 3.VII.1988, Mt. Hakusan, Ishikawa Prefecture, T. Mikage leg. This specimen agrees with the original description by Takeuchi (1959).

Supplementary note.— Sawsheath as in Fig. 19; lancet with 20 serrulae, basal 3 serrulae as in Fig. 31.

Distribution.— Japan (Honshu and Kyushu).

Perineura pictipennis Takeuchi

Perineura pictipennis Takeuchi, 1959: 71.

Specimens examined.— 1 female, 23.IV.1971, Kobotoke, Tokyo Metropolitan, A. Shinohara leg.; 1 female, 19.V.1983, Chugu Spa, foot of Mt. Hakusan, Ishikawa Prefecture, I. Togashi leg.; 1 female, 10.V.1988, Mt. Fujishigadake, Ishikawa Prefecture, I. Togashi leg. These specimens agree with the original description by Takeuchi (1959).

Supplementary note.— Sawsheath as in Fig. 20; lancet with 19 serrulae, basal 3 serrulae as in Fig. 32.

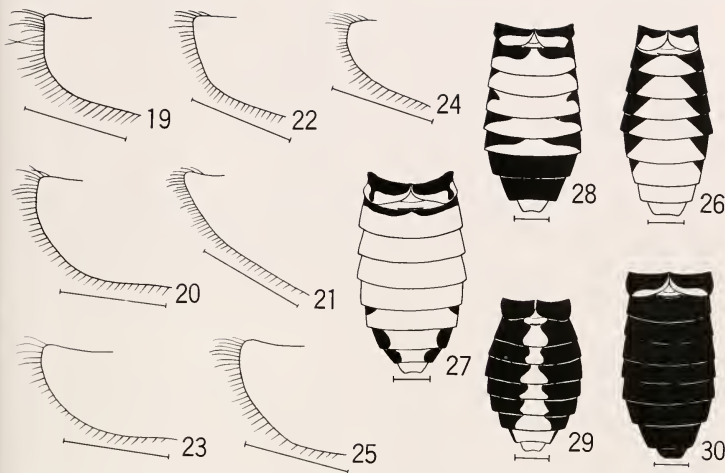
Distribution.— Japan (Honshu, Shikoku, and Kyushu).

Perineura japonica Malaise

Perineura japonica Malaise, 1931: 203.

Specimens examined.— 1 female, 4.VI.1977, Chuzenji, Nikko, Tochigi Prefecture, A. Shinohara leg.; 1 female, 5.VI.1977, Yumoto, Nikko, Tochigi Prefecture, A. Shinohara leg.; 1 female, 26.V.1974, Okutama, Tokyo Metropolitan, A. Shinohara leg.; 1 female, 5.VI.1984, Nojiriko, Nagano Prefecture, A. Shinohara leg.; 1 female, 21-23.VI.1989, Kamikochi, Nagano Prefecture, A. Shinohara leg.; 1 female, 26.V.1974, Ashu, Kyoto Prefecture, A. Mizuno leg. These specimens agree with the original description by Malaise (1931).

Supplementary note.— Mesonotum with some yellow flecks (Fig. 17); sawsheath as in Fig. 21;



Figs. 19-30. 19-25, Sawsheath, lateral view. 19, *Perineura esakii*. 20, *P. pictipennis*. 21, *P. japonica*. 22, *P. stigma*. 23, *P. okutanii*. 24, *P. kamikochiana*. 25, *P. nigra*. 26-30, Color pattern of abdomen. 26, *P. japonica*. 27, *P. stigma*. 28, *P. okutanii*. 29, *P. kamikochiana*. 30, *P. nigra*. (Scale of 19-25, 0.5 mm; 26-30, 1.0 mm.)

lancet with 19 serrulae, basal 3 serrulae as in Fig. 33.

Distribution.— Japan (Hokkaido and Honshu).

Perineura stigma Takeuchi

Perineura stigma Takeuchi, 1959: 72.

Specimens examined.— 1 female, 14.VI.1973, Mt. Hakusan, Ishikawa Prefecture, I. Togashi leg.; 1 female, 14-15.V.1986, Chojabaru, Mt. Kuju, Oita Prefecture, A. Shinohara leg.; 1 female, 1.V.1988, Senomoto, Kumamoto Prefecture, I. Otsuka leg.; 1 female, 3.V.1982, Shiva, Itsuki-mura, Kumamoto Prefecture, I. Otsuka leg.; 1 female, 5.V.1985, Mt. Yamaingiri, Kumamoto Prefecture, I. Otsuka leg. These specimens agree with the holotype.

Supplementary note.— Forewing with a pale brown fleck below stigma (Fig. 13); color pattern of abdomen as in Fig. 27; sawsheath as in Fig. 22;

lancet with 19 serrulae, basal 3 serrulae as in Fig. 34.

Distribution.— Japan (Honshu and Kyushu).

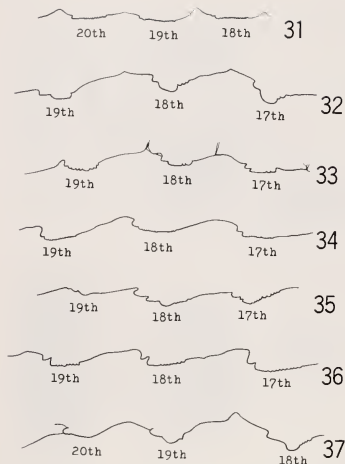
Perineura okutanii Takeuchi

Perineura okutanii Takeuchi, 1959: 73.

Specimens examined.— 1 female, 1.V.1977, Kawachi-mura, Ishikawa Prefecture, I. Togashi leg.; 1 female, 18.IV.1979, Mt. Ryozen, Shiga Prefecture, A. Shinohara leg.; 1 female, 20.V.1981, Jadani, Mt. Daisen, Tottori Prefecture, A. Shinohara leg.; 1 female, 14-15.V.1986, Chojabaru, Mt. Kuju, Oita Prefecture, A. Shinohara leg. These specimens agree with the original description by Takeuchi (1959).

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Figs. 31-37. Basal three serrulae of lancet. 31, *Perineura esakii*. 32, *P. pictipennis*. 33, *P. japonica*. 34, *P. stigma*. 35, *P. okutanii*. 36, *P. kamikochiana*. 37, *P. nigra*.

Supplementary note.— Color pattern of abdomen as in Fig. 28; sawsheath as in Fig. 23; lancet with 19 serrulae, basal 3 serrulae as in Fig. 35.

Distribution.— Japan (Honshu and Kyushu).

ACKNOWLEDGMENTS

I cordially thank Dr. D. R. Smith, U.S. Department of Agriculture, Washington, D.C., for review of the manuscript and Dr. A. Shinohara, the National Science Museum (Natural History), Tokyo, for lending the specimens which are deposited in that Museum. I am indebted to Prof. T. Yasuda and Dr. T. Hirowatari, University of Osaka Prefecture, Sakai, for lending the holotype of *Perineura stigma* Takeuchi, which is deposited in the Entomological Laboratory of the University of Osaka Prefecture. Also, I am indebted to Mr. I. Otsuka, Kumamoto City, Kyushu, for lending me some valuable material.

Revision of the South American Thynnine Genus *Elaphroptera* Guérin-Ménéville (Hymenoptera: Tiphidae)

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Abstract.—The South American thynnine genus *Elaphroptera* Guérin-Ménéville is revised. We recognize 20 species, seven are newly described, including: *boliviana* (Bolivia, Peru), *cuzcoensis* (Peru), *dorada* (Argentina), *fuscata* (Bolivia, Peru), *montifacies* (Brazil), *quadrilobata* (Chile) and *spatulata* (Argentina), and the rest are redescribed. New synonymy is given for *Elaphroptera testaceicauda* Durán-Moya 1941 (= *erythrura* Spinola 1851), and *Elaphroptera holomelas* André 1900 and *racovitzae* André 1900 (= *intaminata* (Smith) 1879). A key to the species is provided and male genitalia are figured for each species.

The thynnine genus *Elaphroptera* Guérin-Ménéville includes some of the largest and most commonly collected members of this subfamily in South America. There are 20 species in this genus. We have not seen any unassignable specimens, but the central Andes are so poorly collected that other species may be found. The species most often encountered in collections and most often commented on in the field are *scoliaeformis* and *nigripennis*.

The biology of this group is largely unknown. *Elaphroptera scoliaeformis*, and a species given as near *nigripennis*, have been reported as parasitoids of scarab beetle grubs: *Aulacopalpus pilicollis* (Fairm.) (Rutellinae) and *Macrosoma glacialis* (F.) (Melolonthinae) respectively (Lloyd 1951).

Members of this genus are large, generally more than 1.5 cm long, darkly colored wasps. Unlike most other thynnines in South America, species of *Elaphroptera* lack yellow or whitish markings.

This genus occurs from Peru and southern Brazil south, along the Andes to southern Chile, particularly in mountainous areas (Fig 1). *Elaphroptera* species group into three geographic regions where their distributions overlap. The Chilean Region, which extends from Coquimbo south to Magallanes Province and through several Andean passes into southwestern Andean Argentina, contains the largest number of species, including: *arcuata*, *atra*, *clypeicarinata*, *erythrura*, *herbsti*, *hyalinipennis*, *intaminata*, *nigripennis*, *quadrilobata*,

sanguinicauda, and *scoliaeformis*. A second group of species occurs in the central Andean region, from southern Peru to Tucuman and Catamarca, Argentina. This group includes: *boliviana*, *cuzcoensis*, *dorada*, *fuscata*, *spatulata* and *strandii*. The final group of species, including: *haematodes*, *montifacies* and *vulpina*, occurs in southern Brazil, from São Paulo to Rio Grande do Sul. We have seen no specimens of these Brazilian species collected more recently than the 1950's and it is quite possible that habitat destruction in this region has resulted in the extinction of one or more of them.

This group has received little revisionary attention in the past 100 years. Brèthes (1910) and Schrottky (1920) placed nearly all the thynnine species they described in *Elaphroptera* without further generic or subgeneric discrimination. Their species grouping was simply reiterated by Turner (1910b) in the Genera Insectorum without further study. Preliminary examination revealed that *Elaphroptera*, as treated by Brèthes and Turner, contained species that belonged in other genera including: *Argenthygnus*, *Brethynus*, *Eucyrtothygnus*, *Glottynus*, *Pseudelaphroptera*, *Spilothygnus*, *Telephoromyia*, and *Zeena*. However, generic synonymy for *Elaphroptera* given below follows that of Turner (1910b).

For a variety of reasons we have not been able to study a number of primary types. André's types should be in Paris, but they cannot be located. We suspect this is because they are either unlabeled as

such, are completely unlabeled, or are actually lost. Some of Spinola's tiphid types, including those discussed herein have apparently been borrowed from Turin and subsequently lost in Rumania. We feel certain of our identification of species where we have not seen primary types either because we have seen other specimens identified by the original author, or because original descriptions and/or illustrations show unique diagnostic features that make recognition of the species straightforward. However, there are three species described as *Elaphroptera*, which we have not been able to study, the primary types are unavailable and the descriptions are vague enough to make even generic recognition impossible. These species are as follow:

Elaphroptera ruficeps Guérin-Ménéville 1838:245. Holotype female; Brazil: Corrientes (GENOA ?).

Elaphroptera tafiensis Brèthes 1910:233. Holotype male; Argentina: Tucumán, Tafí (LA PLATA, type lost). This is probably not a species of *Elaphroptera*, based on the original description since Brèthes states that the male has yellow markings. This species probably belongs in *Eucyrtothynnus* or *Telephoromyia*.

Elaphroptera werner Schrottky 1920:182. Syntype males, females; Paraguay: Puerto Bertoni (type lost). This species is also described as having yellow markings in the male. Also, since Schrottky states that it seems similar to *Elaphroptera anisitsi* Turner (1910a) it is probably a species of *Eucyrtothynnus*.

Phylogenetic relationships between *Elaphroptera* and other South American Thynninae are discussed in detail by Kimsey (1992). *Elaphroptera* belongs with the South American genera remaining in the Thynnini, not those moved into the Scotænini. Although these South American "Thynnini" are probably sufficiently different from the Australasian Thynnini to warrant a separate tribal category. Autapomorphies associated with the male terminalia in *Elaphroptera* indicate that it is the sister group of the other South American Thynnini (Kimsey 1992). Female *Elaphroptera* are relatively unspecialized and do not seem to provide much phylogenetically significant information.

MATERIALS AND METHODS

A large number of species characteristics have been taken from the male genitalia. Terminology used to describe these features is illustrated in Figs. 36-37.

Distributional information includes the months when specimens were collected, indicated by lower case roman numerals enclosed in parentheses.

Specimens used in this study were borrowed from the following individuals and institutions. The name of the contact person is given in parentheses. Type repositories are indicated by the city of the institution given in capital letters at the end of the entry. An asterisk (*) preceding a species entry indicates that the primary type(s) were studied.

ANN ARBOR - Zoology Museum, University of Michigan, Ann Arbor, U.S.A. (M. O'Brien)

BERLIN - Zoologisches Museum an der Humboldt-Universität of Berlin, Germany (F. Koch)

BUENOS AIRES - Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires

CAMBRIDGE - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (J. M. Carpenter, S. R. Shaw)

COPENHAGEN - Zoologisk Museum, Copenhagen, Denmark (O. Lomholdt)

DAVIS - Bohart Museum of Entomology, University of California, Davis, U.S.A. (R. O. Schuster, S. L. Heydon)

EBERSWALDE - Institute für Pflanzenschutzforschung, Eberswalde-Finow, Germany, (J. Oehlke)

GAINESVILLE - Florida State Collection of Arthropods, Gainesville, U.S.A. (L. A. Stange)

GENOA - Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy (V. Raineri)

LA PLATA - Museo de La Plata, Universidad de La Plata, Argentina (R. A. Rondros)

LONDON - Museum of Natural History, London, England (M. C. Day)

LOS ANGELES - Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. (R. R. Snelling)

MUNICH - Zoologische Staatssammlung, Munich, Germany (E. Diller)

NEW YORK - American Museum of Natural His-

- tory, New York, U.S.A. (J. G. Rozen, E. Quinter)
 OXFORD - Hope Entomological Collections, Oxford University, England (C. O'Toole)
 PARIS - Muséum National d'Histoire Naturelle, Paris, France (J. Casevitz-Weulersse)
 SALTA - Manfredo Fritz Collection, Salta, Argentina
 SANTIAGO - Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta D.)
 SÃO PAULO - Museu de Zoologia, Universidade de São Paulo, Brazil (C. R. F. Brandão)
 TUCUMÁN - Fundación Miguel Lillo, Tucumán, Argentina (A. Willink)
 TURIN - Istituto di Zoologia Sistemática, Università di Torino, Torino, Italy (P. d'Entreves, A. Rolando)
 VIENNA - Zweite Zoologische Abteilung, Naturhistorisches Museum, Wien (Vienna), Austria (M. Fischer)
 WASHINGTON - U. S. Museum of Natural History, Washington, D. C., U.S.A. (A. S. Menke)

Genus *Elaphroptera* Guérin-Ménéville

- Elaphroptera* Guérin-Ménéville 1838:214. Type: *Myrmecodes dimidiatus* Haliday 1836:327. Original designation.
Klugianus Ashmead 1903:102. Type: *Thynnus haenatodes* Klug 1842:37. Original designation. Synonymized by Turner 1910b.
Pecnothynnus Ashmead 1903:101. Type: *Elaphroptera atra* Guérin-Ménéville 1839:241. Original designation. Synonymized by Turner 1910b.

Male.—Body length 12–27 mm. Tongue not elongated, maxillary palpus 2–3x as long as stipes; clypeus typically broadly and shallowly emarginate apically, often projecting medially (Figs. 2–19); mandibles usually elbowed submedially, narrowest near base, thickened subapically with small subsidiary tooth (rarely tridentate), inner margin with small triangular projection near bend; scutellum usually subconical in profile; tergum VII apically truncate with straight lateral carinae in dorsal view; sternum VII slender and apically trilobate, tridentate or triangular; genital capsule (Figs. 36–56): gonocoxa strongly projecting dorsally (sunken in

some species) and apex narrowly bilobate, laterally somewhat lobate, gonostylus long and generally slender, apically rounded or tapering, in some species with broadly rounded dorsal lobe; volsella with digitus large and foliaceous (as in Fig. 37), apically cuplike or C-shaped (as in Fig. 45) and cuspis generally foliaceous, toothlike or projecting ventrally (as in Fig. 51); aedeagus with lateral winglike lobes, often with capitate dorsal lobe originating near base of apical loop, and often with a second pair of usually small lobes ventrad of base of apical loop.

Female.—Body length 7–18 mm. Mandible slender, edentate; pronotal disk generally quadrate, wider than long, with long cervical “collar” (as in Figs. 22, 23); propodeum with narrow dorsal surface and somewhat concave posterior face; tergum I with dense brush of setae on anterior surface and small anterolateral tooth, dorsal surface coarsely punctate with distinct transverse carina; tergum II with 2 transverse carinae and rugose between; tergum VI deeply notched laterally, medially evenly curved and rugose, or densely ridged (Figs. 24–30); sternum VI with U-shaped apical lip and slender curved lateral lobe.

Diagnosis.—*Elaphroptera* species are characterized in the male by the elbowed (usually), multidentate mandibles; highly modified, notched, dentate, lobate or nasiform clypeus; and elaborate genital capsule, with elongate dorsoapical lobes on the gonocoxa, aedeagus with apical loop and well-developed lateral lobes, and large foliaceous or strongly angulate digitus. In females diagnostic features are tergum I with a small anterolateral tooth (rarely absent), tergum II rugose between 2 transverse carinae or sulci, and tergum VI broadly ovoid, with vertical rugae or carinae.

Discussion.—This is a highly specialized and divergent genus differing in many ways from other South American Thynninae as discussed by Kimsey (1992). There are a number of autapomorphies of the male head and terminalia, which characterize this group, including: elbowed mandibles, large foliaceous or C-shaped digitus, and small, relatively slender gonostylar lobe. The presence of a dorsal knob on the aedeagus, and the rugose female tergum II suggest a close relationship with *Dolichothynnus* Turner, and perhaps to a lesser

extent with *Chrysothynnus* Turner, *Spilothynnus* Ashmead and *Ammodromus* Guérin-Méneville, as the aedeagus also has ventral lobes in these genera.

Distribution.—This is one of the largest thynnine

genera in South America based on the number of species. *Elaphroptera* is known from Chile, Argentina, Brazil, Peru, Bolivia and Paraguay. The largest diversity of species occur in Chile (Fig. 1).

KEY TO SPECIES OF *ELAPHROPTERA*

1. Wingless, females 2
- Winged, males 19
2. Propodeum with dorsomedial lobe projecting posteriorly, hook-like in lateral view (Fig. 34) 3
- Propodeum without distinct projecting, hook-like dorsomedial lobe (as in fig. 35) 4
3. Tergum VI with rounded lateral angles, broader subapically than basally (Fig. 27) *erythrura* Spinola
- Tergum VI without lateral angles, or lateral angles, broader basally than subapically or parallel-sided for most of length *intaminata* (Smith)
4. Propodeal posterior surface bulging submedially or subapically in lateral view (Fig. 35), tergum VI with angulate lateral lobe (Fig. 24) *hyalinipennis* Spinola
- Propodeum flat, concave, sinuous, or evenly rounded medially in lateral view (as in fig. 33), tergum VI without lateral lobes 5
5. Pronotal dorsum depressed medially from anterior to posterior margin, with two subquadrate lateral lobes, or depressed submedially with elevated medial welt or ridge, nearly planar with anterior collar (as in Figs. 22, 23) 6
- Pronotal dorsum subquadrate and flat or broadly convex, may have short anteromedial depression, elevated above anterior collar 13
6. Pronotum centrally convex, with elevated medial ridge or welt (as in Fig. 23) 7
- Pronotum centrally concave, with short medial welt or ridge (as in Fig. 22) 9
7. Propodeum with dorsal surface longer than scutellum and bulging, posteriorly concave; propleuron flat ventrally (Fig. 21) *dorada*, new species
- Propodeum without dorsal surface, or dorsal surface much narrower than scutellum, posterior surface sloping obliquely from metanotal margin; propleuron convex ventrally (Fig. 20) 8
8. Sternum VI apicolaterally notched *strandi* Turner
- Sternum VI apically sinuous or evenly rounded but not notched *spatulata*, new species
9. Tergum VI: apical rim forming 2 lateral lobes, sternum VI broadly V-shaped *clypeicarinata* Brèthes
- Tergum VI: apical rim not forming 2 lateral lobes, sternum VI apically broadly rounded or truncate, or lateral margin sinuous or notched 10
10. Sternum VI: apicolateral margin sinuous or notched; propodeum with dorsal surface short and narrower than scutellum 11
- Sternum VI: apicolateral margin evenly rounded apicolaterally, propodeum anterior margin as wide or narrower than scutellum, with large dorsally rounded hump 12
11. Sternum VI: apicolateral margin sinuous; propodeal posterior surface appearing saddled when viewed in lateral view (similar to Fig. 21) *montifacies*, new species
- Sternum VI with apicolateral notch; propodeal posterior surface flat in lateral view. *fuscata*, new species
12. Propodeal dorsum narrow, about as broad as scutellum; pronotal collar lower than pronotal disk in

lateral view*arcuata* Turner

— Propodeal dorsum broad, about three times as broad as scutellum; pronotal collar level with pronotal disk*boliviana*, new species

13. Propodeum strongly narrowed anteriorly, as narrow as posterior margin of scutellum in dorsal view 14

— Propodeum broad anteriorly, broader than posterior scutellar margin in dorsal view 15

14. Propodeum with long dorsal surface, longer than scutellum 16

— Propodeum with dorsal surface shorter than scutellum in lateral view*herbsti* André

15. Propodeum posterior surface oblique, sloping posteriorly; tergum VI apical rim U-shaped*nigripennis* (Smith)

— Propodeal posterior surface nearly vertical, tergum VI apical rim V-shaped*quadrilobata*, new species

16. Body length more than 1.5 cm; tergum VI narrowed and tapering apically, rugose area longer than wide (Fig. 29); propodeal declivity convex (Fig. 31)*scoliaeformis* (Haliday)

— Body length less than 1 cm; tergum VI broadly rounded apically, rugose area about as long as broad (Figs. 25, 26); propodeal declivity flat 17

17. Face with large pale spot between eye and antenna; propodeal posterior surface broadly convex, without discrete flattened surface; tergum I evenly rounded above anterior face*cuzcoensis*, new species

— Face without pale spot between eye and antenna; propodeal posterior surface with well defined, broad, flattened area; tergum I conically projecting anteriorly in lateral view*atra* Guérin-Ménéville

18. Three or more basal abdominal segments red or reddish brown 19

— Three or more basal abdominal segments black or dark brown 24

19. Mandible apically tridentate (Fig. 3); clypeus with noselike medial lobe projecting into apical emargination (Fig. 3)*clypeicarinata* Brèthes

— Mandible apically bidentate; clypeus either projecting medially or flat, but without medial lobe projecting into apical emargination 20

20. Abdominal apex black; clypeus nearly flat in lateral view, with triangular, polished medial bevel, apical margin truncate*hyalinipennis* Spinola

— Abdominal apex red; clypeus with small medial projection and apical emargination beveled, or entire, apex projecting strongly outward and up 21

21. Clypeus with small medial knob, apical margin broadly emarginate, with polished bevel and sharp triangular angle on either side of emargination; head and thoracic pubescence black*scoliaeformis* (Haliday)

— Clypeus without medial knob, apical margin strongly arching up and outward, notched or dentate laterally (as in Figs. 15, 16, 19); head and thoracic pubescence golden to silvery 22

22. Clypeal apical margin in lateral view strongly produced into acute medial projection, often appearing slightly hooked at tip and lateral margin slightly sinuous, with broad lateral tooth (Fig. 16); legs black*haematodes* (Klug)

— Clypeal apical margin in lateral view produced into acute or truncate medial projection, not hooked at tip and lateral margin straight or distinctly notched, lateral tooth obtuse or acute; legs mostly red 23

23. Clypeal apical margin truncate in lateral view, with distinct lateral notch (Figs. 7, 15)*montifacies*, new species

— Clypeal apical margin acute in lateral view, with acute lateral tooth, not notch (Fig. 19)*vulpina* (Klug)

24. Clypeus deeply emarginate apically, with long rounded lobes on either side of emargination, mandible with large medial angle on inner margin and large subapical angle on outer margin (Fig. 13) *strandii* Turner
- Clypeus either shallowly emarginate, truncate, strongly projecting anteriorly or lobate apicomediaally, without long lateral lobes; mandible usually without large medial and subapical angles 25
25. Mandibles broad, with large medial angle on inner margin and acute subapical angle on outer margin (as in Figs. 5, 12) 26
- Mandibles slender, without medial or subapical angles 27
26. Clypeus apical margin with medial tooth, not projecting anteriorly (Figs. 12, 14) *spatulata*, new species
- Clypeus apical margin obtusely angulate, not dentate, apical margin strongly projecting, appearing beaklike in lateral view (Figs. 5, 18) *dorada*, new species
27. Clypeal disk flat or broadly convex, without projection above apical margin (as in Figs. 4, 6) ... 28
- Clypeal disk with conical, lobate, acute or toothlike medial projection 30
28. Clypeus without polished apicomediaal area, apical margin of emargination with polished subventral bevel; mandible apically bidentate, with low submedial angle on inner margin (Fig. 6) *fuscata*, new species
- Clypeus with large subtriangular or rounded polished apicomediaal area, apical margin not beveled ventrally; mandible apically bidentate or tridentate, without low submedial angle on inner margin 29
29. Mandible apically tridentate, not elbowed in lateral view, without subbasal angle on inner margin; clypeal polished area triangular (Fig. 4) *cuzcoensis*, new species
- Mandible apically bidentate, elbowed in lateral view, with sharp subbasal angle on inner margin; clypeal polished area rounded *atra* Guérin-Ménéville
30. Mandible apically tridentate, clypeus with rounded medial noselike projection above polished triangular area (Fig. 11); gonostylus short and broadly rounded apically (as in Fig. 57); wings dark brown *nigripennis* (Smith)
- Mandible apically bidentate, clypeus conical or with projecting tooth medially, without large polished area; gonostylus slender and tapering apically (except *arcuata*) (as in Fig. 61); wings light brown or hyaline 31
31. Clypeus strongly projecting medially, with acute, often slightly hooked medial tooth (as in Fig. 17) 32
- Clypeal medial projection conical, without acute medial tooth (as in Fig. 2) 33
32. Clypeal projection not notched laterally, apical margin with two obtuse submedial lobes in front view, body black with extensive red on legs and apical abdominal segments *erythrura* Spinola
- Clypeal projection notched laterally, apical margin with two sharp submedial teeth in front view (Fig. 11) 33
33. Legs and abdominal apex extensively red; mandible with sharp subbasal tooth (Fig. 11); clypeal apex projecting ventrally below noselike medial projection, appearing lip-like (Fig. 11) *sauginicauda* Duran-Moya
- Body entirely black; mandible without sharp subbasal tooth; clypeal apex bidentate, projecting anteriorly below acute medial projection *herbsti* André
34. Clypeal apical margin quadrilobate (easiest to see from beneath), without polished, ventrally beveled apical margin (Fig. 10) *quadrilobata*, new species
- Clypeal apical margin broadly and evenly emarginate, without lobes, apical margin of emargination ventrally beveled (as in Fig. 2) 35
35. Clypeal polished area subtriangular, extending dorsally to medial projection (Fig. 2) *boliviana*, new species

— Clypeal polished area linear along apical margin, widely separated from medial projection.....	36
36. Pubescence of head and thorax pale	<i>arcuata</i> Turner
— Pubescence of head and thorax black.....	<i>intaminata</i> (Smith)

Elaphroptera arcuata Turner
Figs. 30, 32, 36, 57

**Elaphroptera arcuata* Turner 1908:76. Holotype male; Argentina: Patagonia, Chubut, Lago Xanco (LONDON).

Male.—Body length 12-14 mm. Clypeus conical medially, with broad shallow apical emargination and polished bevel ventrally; mandible apically bidentate with small sharp angle subbasally on inner margin, and angular projection submedially, appearing sharply elbowed in lateral view; flagellomere I 2.3 times as long as broad; flagellomere II length three times breadth; scutellum broadly rounded; sternum VII apically trilobate; genital capsule (Fig. 36); gonocoxa dorsomedially projecting and apically bilobate; gonostyle short and rounded, ventral margin concave, with broad rounded dorsal lobe (Fig. 57); digitus small and comma-shaped; cuspis with small rounded outer lobe and large lanceolate inner one next to aedeagus; aedeagus with small slender dorsal lobe, lateral winglike lobes and ventral projection before apical loop. Body entirely black, with silvery to slightly golden pubescence; wing membrane amber-colored.

Female.—Body length 8-9 mm. Frons with narrow ovoid pit at apex of medial sulcus; pronotal disk strongly depressed medially, with large rounded projection on either side, strongly elevated above collar laterally; scutellum considerably narrower than propodeum; propodeum bulbous dorsally, strongly concave laterally and posteriorly (Fig. 32); tergum VI narrowly ovoid posteriorly (Fig. 30); sternum V with posterior setose lobe on either side of VI; sternum VI posterior rim broadly U-shaped. Body dark brown to black with pale spot between eye and antenna.

Diagnosis.—This species closely resembles *intaminata* in both the structure of the male clypeus and genital capsule. *E. arcuata* can be distinguished in the males from those of *intaminata* by having the gonostylus broadly rounded apically and ventrally

emarginate, and pale body setae, and from other *Elaphroptera* by the medially conical clypeus, with the medial projection widely separated from the apical margin, and body entirely black. The female can be distinguished by the medially depressed pronotum, broadly rounded apical tergum and dorsally narrowed and bulging propodeum.

Material examined.—(515 males and 6 females): CHILE: Arauco: 20 km w Caramivda (i); Aysen: Manihuales (i), Coihaique (xii); Bio-Bio: El Abanico (xii); Cautín: Villarrica (xii), Las Raíces (xii), Pucon Peninsula (xi), Termas de Manzanar (xii), 12 km n Loncoche (xii); Chiloe: 30 km s Ancud (xii), Dalcahue (ii), Tepuhueco (xii); Concepcion: Salto de Laja (xii); Curicó: Los Quenes (i); Llanquihue: Petruhue (xi); Magallanes: Laguna Amarga (xii), Parque Nac. Torres del Paine (x); Malleco: Nahuelbuta (xii), Contulmo (i); Nuble: Las Trancas (i), El Marchant (i), Shangri-La (i), Las Cabras (i), Macul (xii) Atacalco (xi), 60 km se Chillán (xii-ii), Macul (xii); O'Higgins: Pilay ne Rancagua (xi); Osorno: La Picada (ii); Santiago: San Ramon (xii), Melipilla (xii), Santiago (xii, i), El Arrayán (xii), Quebrada El Pruno (xi), El Canelo (xi), Quebrada El Manzano (xi, ii); Talca: Alto Vilches (i); Valdivia: 20 km s Valdivia (xi), Valdivia (ii), Curicó (xi); Valparaíso: Valparaíso (i), Renaca (xi). ARGENTINA: Chubut: PN Los Alerces (i), Neuquén: PN Lanín (i), Pucará (xii), Rio Negro: San Carlos de Bariloche (x-xii), El Bolsón (xi), Lago Nahuel Huapi (x), Llao Llao (xii).

Elaphroptera atra Guérin-Ménéville
Figs. 26, 33, 37

Elaphroptera atra Guérin-Ménéville 1838:241.
Holotype male; Chile (GENOA).

Male.—Body length 13-15 mm; clypeus flattened, with broad, shallow apical emargination, lateral angle somewhat rounded, with medial polished and impressed ovoid area extending to apical margin; mandible apically bidentate, with rounded submedial and sharp subbasal angles, appearing

strongly elbowed in lateral view; flagellomere I length 2.5 times breadth; flagellomere II three times breadth; forecoxa with projecting medial hook on inner margin; scutellum broadly rounded; sternum VII trilobate with subapical swelling medially; genital capsule (Fig. 37): gonocoxa dorsomedially sunken toward apex with large, broad apical lobes and small sublateral angle before gonostylus; gonostylus long and tapering apically, widest near base; digitus large and foliaceous, nearly as long as aedeagus, cuspis with rounded apical lobe, flattened and appressed against aedeagus; aedeagus with small dorsal projection and lateral winglike lobes before apical loop. Body entirely black with long silvery pubescence; wings lightly brown stained.

Female.—Body length 8 mm; frons with small circular medial pit; pronotal disk subquadrate, anterior margin slightly impressed, elevated above collar; propodeum with short rounded dorsal surface and flat posterior declivity (Fig. 33); tergum VI broadly rounded apically with thickened and carinate and sinuous lateral edge and transparent apical rim, rugose area about as long as broad (Fig. 26); sternum V not thickened or projecting posterolaterally; sternum VI apical plate broadly V-shaped.

Diagnosis.—This is another species with an all black male with pale setae as in *arcuata*. In the males *atra* appears to be most similar to *erythrura* based on the clypeus having a dorsal polished bevel and apically emarginate, the mandible elbowed with an inner subbasal tooth, the gonocoxa dorsomedially emarginate, and the digitus large and foliaceous. The female more closely resembles that of *nigripennis*, having the pronotum depressed anteromedially, tergum VI with a transparent rim, and the propodeum with a dorsal surface. Males can be distinguished from these and other *Elaphroptera* species by the flat deeply emarginate clypeus with a subtriangular bevel, the forecoxae with a hook on the inner margin, the aedeagus with a dorsal lobe, and both the gonostylus and digitus elongate and foliaceous. Females can be distinguished by tergum I conically projecting anteriorly, the broadly rounded tergum VI, and the face without pale markings.

Material examined.—(191 males and 5 females): CHILE: Aconcagua: Saladilla (xi), San Felipe (x); Aysen: Aysen-Coyhaique (i, iii); Cautín: Pucon (xii); Concepción: Concepción (ix), Salto de Laja (xi); Coquimbo: Pichidandqui (ix, x); Curicó: Cajón de Río Claro (x); Magallanes: Laguna Amarga (xii), Rubes (xii); Malleco: Angol (ix); Santiago: Macul (ix-xi), Santiago (ix, xii), El Peumo (i), El Tabo (x), Maipo (viii), El Portezuelo (xi), El Volcan (ix, xi), Río Colorado Maipo Canyon (x), Cuesta la Dormida (xi), Tiltit (xi), El Arrayán (xi), Melocoton (x), El Canelo (xi); Valparaíso: Los Perales (x), Valparaíso (viii, x).

***Elaphroptera boliviana* Genise and Kimsey,**
new species
Figs. 2, 38, 58

Male.—(Holotype) Body length 18 mm; forewing 16 mm; clypeus broadly conical medially, with broad deflexed polished bevel extending to apex of cone (Fig. 2); mandible apically bidentate, without angles or teeth on inner margin, appearing evenly curved in lateral view (Fig. 2); scutellum strongly elevated and subconical; sternum VII apically tridentate; genital capsule (Fig. 38): gonocoxa depressed dorsomedially ending in two large lobes, with sharp angle on either side before gonostylus; gonostylus less than twice as broad as long and tapering apically, broadest subbasally (Fig. 58); digitus foliaceous, long and tapering apically, broadest submedially; cuspis flattened and appressed against aedeagus; aedeagus with small dorsal lobe and two winglike lateral lobes before apical loop. Body entirely blackish with long pale yellowish setae; wings faintly brown stained. Paratypes are structurally similar to type except varying in body length from 11–18 mm, and the forewing length 10–19 mm.

Female.—Body length 11–13 mm; genal region evenly rounded ventrally; pronotal disk subquadrate, bulging laterally, sunken and even with collar medially; propodeum with bulging dorsal surface, evenly rounded to slightly concave posterior surface; tergum VI rugose area wider than long, apicomediaally with smooth translucent rim; sternum VI posterior rim broadly U-shaped; body dark

brown with broad pale band across antennal sockets.

Diagnosis.—Two species, *boliviana* and *cucensis* have similar males, and may be closely related. Males of both have the mandibles straight, without an inner tooth, the digitus and gonostylus are large and foliaceous, and the aedeagus lacks a dorsal lobe. *El. boliviana* can be distinguished by the apically bidentate mandibles, clypeal emargination V-shaped, with shallow broad apical bevel, and gonocoxa without ventral carinae. Female *boliviana* most closely resemble those of *montifacies* and less so *arcuata*, based on the structure of the pronotum and propodeum, but can be distinguished from them by the evenly rounded tergum VI and dorsally broad propodeum.

Etymology.—This species is named for its country of collection.

Types.—Holotype male: BOLIVIA: Cochabamba Prov., Coari, 3500 m, Foerster, Mar. 1957 (SALTA). Paratypes 49 males and 3 females: Cochabamba Prov.: 1 male, Siberia, 2900 m, L. Peña, Feb. 1976 (BUENOS AIRES); 2 males, Aquirre, M. Fritz, Feb. 1971 (SALTA); 1 male, Coari, 3500 m, J. Foerster, Mar. 1957 (BUENOS AIRES); La Paz Prov.: 3 males, La Paz, 4000 m, Nov. 1905, Magretti collection (GENOA, DAVIS); 1 male, Altiplano, Pillapi, 70 km e La Paz, 3780 m, 14-17 April 1964, in field of alfalfa and grass, J. L. Chudley (LONDON); 2 females, 14 males, Río Mauri, General Campero, 13-14 Feb. 1954, W. Forster (MUNICH, DAVIS, BUENOS AIRES); 1 female, Yungas de Corani, 2500 m, 30 Sept. 1953, W. Forster (MUNICH); Potosi Prov.: 2 males, E. Ocuri, 4000 m, L. Peña, Feb. 1976 (SALTA); 11 males, 50 mi n Potosi, 22 Feb. 1951, Ross & Michelbacher (DAVIS, SAN FRANCISCO); 1 male, Yocona, 3500 m, L. Peña, Feb. 1976 (SALTA); 7 males: Pacajes Prov., near Caquiaviri, 4000 m, March 1983, S. Keen (ANN ARBOR, DAVIS); PERU: Puno Prov.: 3 males Puno, May 1937, J. Soukup (NEW YORK); 1 male, 10 mi n Ayaviri, Jan./Mar. 1951, Ross & Michelbacher (SAN FRANCISCO), Puno, 3900 m, Weyrauch, Dec. 1940 (TUCUMAN); Cuzco Prov.: 1 male, Machu Pichu, 2400 m, Weyrauch, Jan. 1969 (TUCUMAN).

Elaphroptera clypeicarinata Brèthes

Figs. 3, 39

**Elaphroptera clypeicarinata* Brèthes 1910:242.
Holotype male; Argentina: Chubut (BUENOS AIRES).

Male.—Body length 21-23 mm; clypeus apically trilobate with medially protruding rounded lobe, projecting into apical emargination, emargination with broad ventrally curved bevel (Fig. 3); mandibles apically trilobate, with sharp submedial angle on inner surface, appearing nearly straight in lateral view; flagellomere I twice as long as broad; flagellomere II 2.4 times as long as broad; scutellum strongly projecting and rounded dorsally; sternum VII subtriangular apically with strong medial lobe; genital capsule (Fig. 39); gonocoxa strongly produced dorsomedially projecting apically into two large foliaceous lobes, each slightly bending laterally; gonostylus elongate, apically rounded and narrowest basally, with separate, low subtruncate dorsal lobe at base of digitus; digitus broadly elbowed, wrapping around dorsal gonocoxal lobes; cuspis closely appressed to venter of aedeagus; aedeagus with acute, elongate and apically capitate ventral lobe, and lateral lobes enlarged, apically bilobate and cupping apical lobes of gonocoxa. Head, thorax and legs black with black pubescence; abdomen red with pale setae; wing membrane amber-colored.

Female.—Body length 8-9 mm; frons with deep medial sulcus; gena rounded ventrally; pronotal disk depressed medially, abruptly elevated above collar; scutellum slightly elevated above propodeum in lateral view; dorsal surface of propodeum short, rounded and elevated, posterior surface concave; sternum V posterolateral corners not projecting, but with group of long hairs; tergum VI with longitudinal rugulae and punctures, apical rim forming two lateral lobes; sternum VI rim broadly V-shaped. Body black, paler on mandibles and antennae; frons with large yellow area above antennae and between eyes.

Diagnosis.—Although this large wasp, with a red abdomen in the males, superficially resembles *scoliaeformis* it appears to be most closely related to *hyalinipennis* and *nigripennis*, based on the

following derived features: the C-shaped digitus, and elaborate cuspis with large well-developed ventral lobe. *E. clypeicarinata* can be distinguished in the male by having the mandibles apically tridentate and not elbowed, and clypeus emarginate with a medial lobe projecting into the emargination, and no apical bevel. The laterally lobate tergum VI and V-shaped sternum VI are the most distinctive features of female *clypeicarinata*.

Material examined.—(90 males and 3 females): ARGENTINA: Chubut: El Bolsón, Lago Puelo (xi, xii), Neuquén: Pucará, San Martín de los Andes (xii), Río Negro: Bariloche (xi), Llao Llao (xii), 4 km s Puerto Moreno (xi); CHILE: Aysen: Lago Frio (i), Coihaique (xii).

Elaphroptera cuzcoensis Genise and Kimsey,
new species
Figs. 4, 25, 40

Male.—(Holotype) Body length 19 mm; forewing 17 mm; clypeus broadly convex with large polished triangular area medially, ventral margin without transverse bevel (Fig. 4); mandible apically tridentate without angulate inner margin, nearly straight in lateral view; scutellum broadly conical; sternum VII apically trilobate; genital capsule (Fig. 40); gonocoxa deeply emarginate dorsomedially, with sharp tooth or angle on either side before gonostylus, strongly produced ventrally with 2 submedial carinae; gonostylus slender and tapering apically, widest medially; digitus long and tapering apically; cuspis foliaceous, appressed to aedeagus; aedeagus with large hooked lateral lobe and low ventral lobe before apical loop. Body entirely black with long pale silky setae, becoming browner on dorsum of head and thorax.

Female.—Body length 11 mm; genital region evenly rounded ventrally; pronotal disk subquadrate, elevated above collar; propodeum with long dorsal surface evenly rounded to posterior surface; tergum VI apically broadly rounded, laterally sinuous, coarsely rugose area as broad as long (Fig. 25); sternum VI posterior rim broadly U-shaped. Body dark brown, with large yellow spot between eye and antenna.

Diagnosis.—*E. cuzcoensis* appears to be closely related to *boliviana*, as discussed under that spe-

cies. However, *cuzcoensis* males can be distinguished by the apically tridentate mandibles, clypeal emargination evenly concave, with a short broad subtriangular apical bevel, and gonocoxa with ventral carinae. Females can be recognized by the coarsely reticulate and apically broad tergum VI and posteriorly convex propodeum.

Etymology.—This species is named for the collection site of the types in Cuzco, Peru.

Types.—Holotype male: PERU: Cuzco, Akanacu, 1 November 1963 (WASHINGTON). Paratype female: same data as type (WASHINGTON).

Elaphroptera dorada Genise and Kimsey,
new species
Figs. 5, 18, 21, 23, 41

Male.—(Holotype) Body length 12 mm; forewing length 11 mm; clypeus strongly projecting apically, with apical rim extending to apex of projection, appearing beaklike in lateral view, with lateral tooth (Figs. 5, 18); labrum inserted considerably basad of clypeal apex; mandible apically bidentate, broadened submedially with large rounded ventral angle and broadly obtuse dorsal one; flagellomere I 2.2 times as long as broad; flagellomere II length 2.4 times breadth; scutellum broadly conical; sternum VII apex with sharp medial lobe and 2 rounded lateral ones; genital capsule (Fig. 41); gonocoxa dorsomedially sunken between large sublateral lobes, ending apically in two subrhomboid lobes; gonostylus slightly widened medially, tapering apically; volsella; digitus large and lanceolate, more than twice as long as broad, cuspis flattened, appressed to aedeagus; aedeagus with large membranous lateral lobe before apical loop. Body black, with gold pubescence; wing membrane lightly brown tinted. Paratype males vary in body length, 11–16 mm.

Female.—Body length 6–10 mm; face with medial sulcus extending ventrally from small frontal pit; thorax (Figs. 21, 23) propleura flattened ventrally; pronotal disk subtriangular, anteriorly trilobate, with medial ridge extending onto collar, submedially depressed; scutellum bulging, elevated above propodeum; propodeum with small rounded dorsal surface, concave posteriorly; sternum V

unmodified; tergum VI rugose posterior surface broadly ovoid, with membranous lateral rim ending apicomediaally. Body dark brown to black with pale spot between eye and antennal socket.

Diagnosis.—The male mandible and genitalia, and female propodeum and pronotal disk suggest a close relationship with *spatulata*. However, this species can be clearly distinguished from *spatulata* and other *Elaphroptera* species by the male clypeus, coloration, and gonocoxa. Female *dorada* can be recognized by the pronotum having a medial welt, the dorsally bulging propodeum, and ventrally flat propleura.

Etymology.—This is a nonsense name.

Types.—Holotype male: ARGENTINA: Catamarca, Capillitas, February 1987, 2600 m (SALTA). Paratypes: 29 males and 19 females; 24 males and 19 females, same data as type; 5 males: Tucumán, Tafí del Valle, and El Suncho, March 1956 (BUENOS AIRES, DAVIS, SALTA, TUCUMAN).

***Elaphroptera erythrura* Spinola**

Figs. 27, 34, 42

Elaphroptera erythrura Spinola 1851:295. Holotype male; Chile (TURIN ?).

Elaphroptera relicta Saussure 1867:126. Holotype female; Chile (VIENNA ?). Synonymized by Turner 1910b.

Elaphroptera testaceicauda* Durán-Moya 1941:151. Lectotype male (desig. by Kimsey and Brown 1993); Chile: Limache (EBERSWALDE). **New synonymy.

Male.—Body length 14–15 mm; clypeus with sharp slightly hooked medial projection, appearing nose-like in lateral view, apical emargination broad and shallow, with small triangular flattened medial area on apical margin, and ventral bevel; mandible apically bidentate with obtusely rounded area on inner margin subbasally, strongly elbowed in lateral view; flagellomere I 2.3 times as long as broad; flagellomere II length 2.6 times breadth; scutellum broadly rounded; sternum VII trilobate apically; genital capsule (Fig. 42); gonocoxa sunken dorsomedially, with large angulate lateral lobe before gonostylus and narrow apical lobes basally

constricted; gonostylus long, slender and tapering apically; digitus long and slender; cuspis with small lateral lobe and inner lobe appressed to aedeagus; aedeagus with pale lateral lobes before apical loop. Head, thorax, fore and midfemora and abdominal segments I–V black; apical abdominal segments, rest of legs and mandibular apices red, with long silky pale setae; wing membrane faintly brown-stained.

Female.—Body length 9–10 mm; frons with irregular depression as apex of medial sulcus; gena strongly angulate ventrally; pronotal disk subquadrate, abruptly elevated above collar; propodeum with strong dorsomedial projection, appearing hooked in lateral view and strongly concave posteriorly (Fig. 34); sternum V posterolateral angle with long setae; tergum VI broadly ovoid posteromedially, carinate laterally with apical margin thin and transparent, broadly lobate laterally (Fig. 27); sternum VI broadly V-shaped, with digitate lateral lobe. Body reddish brown, face paler near eyes.

Diagnosis.—Although there are several Brazilian species with males having a strongly projecting nose-like clypeus, in these species the apex of this projection is actually the clypeal margin. In *erythrura* and *herbsti* the clypeus strongly projects in a somewhat similar fashion, however, the projection is actually above the clypeal margin. Males of these two Chilean species can be separated by the red apical abdominal segments in *erythrura*, and the laterally notched clypeal margin, with sharp submedial teeth, and aedeagus with a dorsal lobe in *herbsti*. Although the type of *erythrura* is unavailable and that of *relicta* cannot be located the original authors descriptions are sufficient to recognize these species and *testaceicauda* is clearly synonymous. The posteriorly hooked propodeum and laterally angulate tergum VI will immediately distinguish female *erythrura*.

Material examined.—(186 males and 10 females): CHILE: Aconcagua: Saladillo (xi); Coquimbo: Coquimbo (ix, x), Punitaqui (viii); Curicó: Los Quenes (x); Santiago: El Canelo (x–xii), Macul (xi), Santiago (x, xii, i), El Peumo (i), Maipú (viii), Quilicura (x), Renca (xii), Tiltill (xi), Lo Prado (xi); Valparaíso: Cuesta Pucalán (ix), Valparaíso (viii, ix).

Elaphroptera fuscata Genise and Kimsey,
new species
Figs. 6, 43, 59

Male.—(Holotype) Body length 14 mm; clypeus somewhat convex in lateral view, with broad shallow apical emargination, lateral angle sharp, medial area smooth and ventral margin beveled (Fig. 6); mandible apically bidentate, with subapical swelling on inner margin, appearing evenly curved in lateral view; flagellomere I length 2.5 times breadth; flagellomere II length 2.8 times as long as broad; scutellum broadly conical in lateral view; sternum VII apically trilobate; genital capsule (Fig. 43); gonocoxa dorsomedially sunken between sharp sublateral lobes, with elongate basally constricted apical lobes; gonostylus broadest submedially and strongly tapering apically (Fig. 59); digitus broadly foliaceous; cuspis flattened and appressed to aedeagus; aedeagus with membranous lateral lobes before apical loop. Body black with long pale yellowish setae, wing membrane brown-stained.

Female.—Body length 10 mm; face with medial sulcus extending downward from small round frontal pit; pronotal disk strongly sunken medially, bulging laterally into large lateral lobe, medially planar with anterior collar; prothorax strongly dorsoventrally compressed; scutellum strongly compressed laterally; propodeum with short dorsal surface, flattened posteriorly; tergum I anteromedially sharp-edged, forming a right or acute angle in lateral view; sternum V unmodified; tergum VI rugose posterior surface as broad as long or broader, apex narrowly produced and truncate; sternum VI apical rim trilobate, notched sublaterally. Body dark brown, with lower half of face, across eyes, pale.

Diagnosis.—This species can be distinguished in males by the flattened and shallowly emarginate clypeus, mandibles evenly curved and without an inner subbasal tooth, the gonocoxa is dorsomedially sunken, and the aedeagus lacks a dorsal or ventral lobe. *E. fuscata* appears to be most closely related to *cuzcoensis* and *boliviana*, based on the structure of the male clypeus, mandibles and genital capsule. The clypeus is most like that of *boliviana* except that the apical margin is sharply polished, with a discrete ventral bevel. The gonocoxa has ventral

carinae as does *cuzcoensis*, however, the dorsomedial lobes are blunt unlike the condition in these other species. In addition, *fuscata* has the gonostylus strongly expanded medially. Females can be distinguished by the prothorax medially depressed and dorsoventrally compressed, tergum I anteriorly sharply angulate in lateral view, sternum VI apically trilobate, and tergum VI narrowly produced and truncate apically.

Etymology.—The species name refers to the dark body and wing color of the male.

Types.—Holotype male: BOLIVIA: Cochabamba, 55 km se Villa Tunari, Carretera Cochabamba, 25 July 1973, C. Porter, L. Stange and E. Demarest (TUCUMAN). Paratypes: 3 males: BOLIVIA: La Paz, Chulumani, 5 April 1979, M. Cooper (LONDON); 2 males and 2 females: same data as type (GAINESVILLE, BUENOS AIRES, TUCUMAN); 9 males: PERU: Machu Pichu, 1900 m, 4-19 September 1964, C. C. Porter (DAVIS, CAMBRIDGE).

Elaphroptera haematodes (Klug)

Figs. 7, 16, 44

**Thynnus haematodes* Klug 1842:37. Lectotype male (design. by Kimsey and Brown, 1993); Brazil: Cassapava (BERLIN).

Male.—Body length 15-17 mm; clypeal apical margin strongly projecting medially, forming an acute angle in lateral view and appearing slightly hooked at tip, with obtuse lateral notch followed by a rounded basal tooth, ventral bevel large and triangular in ventral view (Figs. 7, 16); mandible apically bidentate with small sharp subbasal tooth on inner margin, strongly elbowed in lateral view (Fig. 7); flagellomere I twice as long as broad; flagellomere II length 2.5 times breadth; scutellum broadly conical in lateral view; genital capsule (Fig. 44); gonocoxa dorsomedially sunken toward apex with sunken dorsoapical lobes short and apically angulate, with large sublateral lobe before gonostylus; gonostylus narrowly triangular, slightly constricted before base; cuspis closely appressed to aedeagus; digitus large and foliaceous; aedeagus with large membranous lateral lobes before apical loop and small dorsal angle or tooth. Head, thorax

and legs black; abdomen dark red with segment I basally black and apical segments darker red to blackish; pubescence long and pale; wing membrane amber-colored.

Diagnosis.—Males of three Brazilian species, *haematodes*, *montifacies* and *vulpina* all closely resemble one another, having a black head and thorax, with pale setae, and brownish red abdomen. *E. vulpina* and *montifacies* also have reddish legs, although leg color is of questionable value. The primary differences among these species involve modifications of the clypeus and genital capsule. In *haematodes* the clypeal margin appears slightly hooked at tip and is slightly sinuous laterally, with broad lateral tooth when viewed laterally. The others have the tip of the projection not hooked and the lateral margin is either straight or distinctly notched, with an obtuse or acute lateral tooth.

Material examined.—(5 males): BRAZIL: Rio Grande do Sul: Arroio Arapua, Pelotas (x), "Cassapava".

***Elaphroptera herbsti* André**

Fig. 45

Elaphroptera herbsti André 1904:308. Holotype male; Chile: Concepción (PARIS ?).

Male.—Body length 15-16 mm; clypeus with large, thin, sharp medial tooth-like projection, slightly hooked in lateral view, apical emargination broad and deep with large wide sublateral notch before lateral tooth, and large ventral bevel; mandible apically bidentate with subapical swelling and small subbasal obtuse angle on inner margin, strongly elbowed in lateral view; flagellomere I and II 2.6 times as long as broad; scutellum obtusely rounded in lateral view; sternum VII apically trilobate; genital capsule (Fig. 45); gonocoxa dorsoapically elongate, ending in long slender lobes; gonostylus long and slender, tapering apically, with low dorsal lobe; digitus cylindrical and C-shaped; cuspis apically broad and truncate; aedeagus with large transparent lateral lobes and long digitate dorsal lobes before apical loop. Body entirely black with long yellowish setae; wing membrane faintly brown-stained.

Female.—Body length 8-9 mm; frons without distinct pit at apex of medial sulcus; gena strongly angulate ventrally; pronotal disk subquadrate, abruptly elevated above collar; scutellum elevated above propodeum; propodeum with short dorsal surface before oblique posterior slope, with obtuse subapical and subbasal swelling or angle; sternum V without apicolateral lobe or angle; tergum VI apical rugose surface ovoid, with wide transparent apical rim; sternum VI with broadly U-shaped apical rim. Body dark brown, with pale maculae on face.

Diagnosis.—As discussed under *erythrura*, *erythrura* and *herbsti* are closely related. *E. herbsti* males can be separated by the red apical abdominal segments, the clypeal margin notched laterally, with two sharp submedial teeth when viewed anteriorly, and aedeagus with a dorsal lobe. Females are distinguished by the propodeum having a short and strongly narrowed dorsum followed by an oblique posterior slope, and a nearly flat pronotal dorsum.

Material examined.—(36 males and 9 females): CHILE: Arauco: Quillota (ix); Concepción: Lirquen (x), Concepción (ix, x); Coquimbo: Los Vilos (x), Talinay (vii); Malleco: Nahuelbuta National Park (ix), Angol (x); Valparaíso: Valparaíso (xi).

***Elaphroptera hyalinipennis* Spinola**

Figs. 24, 35, 46, 60

Elaphroptera hyalinipennis Spinola 1851:296. Holotype male; Chile (TURIN ?).

Male.—Body length 19-23 mm; clypeus apically subtruncate with large triangular apicomedial polished area above apical margin, bulging slightly medially; mandible apically bidentate without teeth or angles on inner margin, evenly curved in lateral view; flagellomere I length 2.3 times breadth; flagellomere II 2.6 times as long as broad; scutellum apically indented or bilobate, conical in lateral view; sternum VII apically with sharp medial tooth and right angle laterally; genital capsule (Fig. 46); gonocoxa dorsomedially bulging and elongate, apical lobes narrowed basally and broadly separated apically; gonostylus short, broad and rounded apically, narrowest basally, with obtuse low dorsal lobe (Fig. 60); digitus strongly elbowed, apically

cuplike around aedeagus and cuspis; cuspis appressed to aedeagus; aedeagus with dorsal digitate projection and long ventral lobes below apical loop. Head, thorax and legs black; abdomen red except segment I basally and VI and VII black, pubescence erect and golden; wing membrane amber-colored.

Female.—Body length 7–10 mm; frons with deep medial sulcus; gena rounded ventrally; pronotal disk with an anteromedial depression, abruptly elevated above collar; scutellum rounded, more elevated than dorsal surface of propodeum; propodeum with conical posteromedial elevation on dorsal surface, posteriorly flattened (Fig. 35); sternum V posterolateral corners unmodified; sternum VI broadly U-shaped; tergum VI with angulate lateral angles and a narrow posterior plate (Fig. 24). Body light brown, darker on thorax, yellow areas above antennae between eyes, gena and posterior margin of vertex (more visible on some specimens than others).

Diagnosis.—This species appears to be related to *nigripennis* and *clypeicarinata* as the male genitalia are quite similar among the three species. *E. hyalinipennis* males can be distinguished from those of *nigripennis* and *clypeicarinata* by the flat clypeus medially with a large, polished triangular area, mandibles not elbowed and without subbasal tooth on inner margin, and abdomen red except the base of segment I and segments VI and VII. The female of *hyalinipennis* most closely resembles that of *intaminata*. It can be distinguished from that and other species by having the propodeum bulging medially and tergum VI with an angulate lateral lobe.

Material examined.—(521 males and 35 females): CHILE: Arauco: Caramavida (ii), Contulmo (xii, ii); Aysen: Puerto Cisnes (ii), Lago Frío (i), Balmaceda (i), Aysen (i), Río Manihuales (i), 16 km nw Cisnes Medio (xii-ii); Cautín: Volcan Villarrica (xii), n shore Lago Villarrica (xi, xii), 30 km ne Villarrica (i), Termas de Manzanar (xii), Nueva Imperial (i), Cudico (i), 21 km ne Pucon (xii-ii), 15 km ne Villarrica (xii-ii), La Selva w Temuco (xii), Lago Caburga (i); Chiloe: Dalcahue (i); Llanquihue: Lago Chapo (xi); Malleco: Curacautín (iii), 40 km w Angol (xii-ii), Puren (xii-ii), Victoria (xii-ii), Nahuelbuta National Park (ii); Osorno: Puyehue (xii-iii), Anticura (iii), 8 km w La Picada

(ii), Río Golgol (x, iii), 30 km e Purranque (i); Santiago: Santiago (x); Valdivia: Valdivia (xi-iii), Anticura (ii), Puerto Fui (iii); ARGENTINA: Chubut: PN Los Alerces (ii), Lago Mendez (i, ii); Neuquén: PN Lanín (x-iii), Pucará (xii, i), Lago Lacar (xi), Bajada de Rahue (iii); Río Negro: El Bolsón (xi).

Elaphroptera intaminata (Smith)

Fig. 47, 56

**Thynnus intaminata* Smith 1879:173. Holotype male; Chile (LONDON).

Thynnus holomelas André 1900:105. Holotype female; Chile: Patagonia, Cerro de Ultima Esperanza, Magellanes (PARIS, lost?). [Non-type material labeled by André was studied].

New synonymy.

Thynnus racovitzi André 1900:105. Holotype male; Chile: Patagonia, Cerro de Ultima Esperanza, Magellanes (PARIS, lost?). [Non-type material of André's was studied]. **New synonymy.**

Male.—Body length 14–16 mm; clypeus densely and finely punctate, conically produced anteriorly, apex of cone located well above apical margin, apical margin broadly emarginate with sharp lateral angle, and smooth ventral bevel; mandible apically bidentate, with small secondary tooth and small subbasal angle on inner margin, elbowed in lateral view; flagellomere I length 2.3 times breadth; flagellomere II 3 times as long as broad; scutellum broadly rounded; sternum VII evenly trilobate apically; genital capsule (Fig. 47): gonocoxa dorsally projecting apically in long sharp apical lobes; gonostylus parallel-sided, slightly curved ventrally and broadly rounded apically, with broad rounded dorsal lobe; digitus bilobate with slender curved apical lobe and rounded basal lobe; cuspis with strong ventrally projecting lobe apically; aedeagus with lateral winglike lobes, long slender dorsomedial projection and broad ventromedial lobes before apical loop (Fig. 56). Body black, with long black pubescence; wing membrane amber-colored.

Female.—Body length 7–9 mm; face with medial sulcus extending ventrally from small round frontal pit; gena rounded ventrally; pronotal disk subquadrate, divided by a broad medial depression

and nearly planar with collar; scutellum strongly bulging dorsally and compressed laterally; propodeum dorsal surface bulging and knoblike, posterior surface strongly concave; sternum V posterolateral corners projecting beside tergum VI; sternum VI broadly V-shaped; tergum VI rugose posterior face subrectangular, with thin transparent rim. Body dark brown to black, paler above antennae between eyes.

Diagnosis.—The structure of the male clypeus and genital capsule indicates a close relationship with *arcuata*. *E. intaminata* males can be distinguished by the slender gonostylus, and black body setae, and from other *Elaphroptera* by the characteristics discussed under *arcuata*. Females are fairly unmodified, but can be identified by the medially depressed pronotum, and the propodeum dorsally bulging and knoblike, and strongly concave posteriorly.

Material examined.—(315 males and 40 females): CHILE: Chiloe: Puntra (xii), Queilon (xii); Concepción: Salto de Laja (xi); Curicó: Los Quenes (x), El Coigual (x), Las Trancas (iii); Llanquihue: Salto Petrohue (xii); Magallanes: Puerto Natales (xii), Laguna Amarga (xii); Malleco: Las Raíces (xii), Victoria (i); Maule: Cauquenes (xii); Nuble: Recinto (xii-ii), Las Trancas (xii-ii), Las Comadres near Chillán (ii); O'Higgins: Rancagua (xi); Osorno: Puyehue (x), Osorno (ix); Santiago: Santiago (i), Quebrada El Prumo (xi), El Manzano (xi); Talca: Alto Vilches (xii-ii); Valdivia: 20 km se Valdivia (ii), Valdivia (x-xii); Valparaíso: Valparaíso (xi); ARGENTINA: Chubut: PN Los Alerces (i), PN Lanín (x-iii); Río Negro: Bariloche (xi).

***Elaphroptera montifacies* Genise and Kimsey,**
new species

Figs. 8, 15, 48, 61

Male.—(Holotype) Body length 17 mm; clypeus broadly and deeply emarginate with deep lateral notch, entire apex projecting anteriorly, appearing truncate in lateral view, medially slightly concave with broad ventral bevel (Figs. 8, 15); mandible apically bidentate with small sharp subbasal angle on inner margin, appearing elbowed in lateral view; flagellomere I length 2.3 times breadth; flagellomere II 2.5 times as long as broad; scutellum conical in

lateral view; sternum VII apically tridentate; genital capsule (Fig. 48); gonocoxa dorsomedially sunken between large sublateral lobes, with large rounded apical lobes; gonostylus elongate, slender and tapering apically (Fig. 61); digitus elongate, 3.5 times as long as broad, with slender basal half; cuspis flattened and appressed to aedeagus; aedeagus with dorsal knob and lateral membranous lobes at base of apical loop. Head and thorax black with red on mandible, 2 small spots at top of eyes, posterior pronotal margin, tegulae, fore and midfemoral apices, tibiae, tarsi and hindleg; abdomen red, except base of segment I; wing membrane amber-colored, veins dark red.

Female.—Body length 10 mm; face with deep medial sulcus; genal area rounded ventrally; pronotal disk broadly subquadrate, shallowly depressed anteromedially, with low medial ridge and level with collar; scutellum lower than dorsum of propodeum; propodeum with narrow projecting dorsal surface, posteriorly concave subapically, bulging below; sternum V without posterolateral lobes or projections; tergum VI tapering apically with wide transparent rim; sternum VI apical plate broadly U-shaped. Body reddish brown, paler on face, flagellum, tibiae and tarsi; thorax nearly black.

Diagnosis.—As discussed under *haematodes*, that species, *montifacies* and *vulpina* appear to be closely related, and, in males, the projecting, nose-like clypeal margin will immediately separate these species from all others. In *montifacies* the clypeal margin is truncate in lateral view with a distinct lateral notch, not a tooth as in the other two species. Females have the pronotum sunken medially, which aligns them structurally with *clypeicarinata*, *arcuata* and *boliviana*. In addition, *montifacies* females have the propodeum with a narrow dorsal lobe and saddled posteriorly, and the apicolateral margin of sternum VI is sinuous.

Etymology.—This name refers to the strongly protruding, "mountain"-like appearance of the male face in lateral view.

Types.—Holotype male: BRAZIL: Santa Catarina, Nova Teutonia, November 1960, F. Plaumann (DAVIS). Paratypes: 18 males, same data as type, except various dates: September 1964, February 1966 (DAVIS, SÃO PAULO, CAMBRIDGE); 2 males: Theresopolis, F. Schneider

(COPENHAGEN); 20 males and 5 females: Río Grande do Sul, Stieglmayr (VIENNA, DAVIS).

***Elaphroptera nigripennis* (Smith)**

Figs. 9, 49

**Thynnus nigripennis* Smith 1879:172. Lectotype male (desig. by Kimsey and Brown, 1993); Chile (LONDON).

Male.—Body length 20-24 mm; clypeus with rounded noselike medial projection, with subtriangular polished and somewhat concave bevel bounded laterally by rounded ridge, apical margin subtruncate medially with sharp sublateral tooth at apex of each ridge (Fig. 9); mandible apically tridentate, with obtuse projection on both inner and anterior surface, making mandible appear elbowed in lateral view; scutellum rounded conical in lateral view; flagellomere I length 2.2-2.4 times breadth; flagellomere II 2.5-2.6 times as long as broad; sternum VII apically trilobate; genital capsule (Fig. 49): gonocoxa dorsomedially projecting into slender slightly curved apical lobes; gonostylus short and subquadrate, only slightly wider apically than at base, with broad subtruncate dorsal lobe; digitus slender and C-shaped; cuspis toothlike with two dorsal lobes; aedeagus with dorsal knob, membranous lateral lobes and slender, long, well developed ventral lobes before apical loop. Body entirely black with long black pubescence; wing membrane dark brown.

Female.—Body length 8-11 mm; frons with deep medial sulcus; gena evenly rounded ventrally; pronotal disk subquadrate, slightly indented anteriorly, abruptly elevated above collar; scutellum elevated above propodeum; propodeum with rounded dorsal surface, posterior surface bulging dorsally and concave below on other side of medial welt or ridge; sternum V without posterolateral projection; tergum VI rugose surface broadly ovoid with wide transparent apical rim; sternum VI posterior rim broadly U-shaped. Body dark brown to black with yellow maculae on face between eye and antennal socket.

Diagnosis.—This is the largest of the all species with black males, males of other black species are less than 2 cm long. It is commonly encountered in

Andean Argentina and mountane Chile. Aside from the large size and relatively dense black setae on the male body, *nigripennis* can be recognized by the structure of the male clypeus, which is apically truncate, with a small rounded medial projection, subtended by a depressed polished and ventrally sharp-edged area. The C-shaped digitus suggests a close relationship with *arcuata*, *clypeicarinata*, *intaminata* and *hyalinipennis*. *E. nigripennis* is probably most closely related to *hyalinipennis* and *clypeicarinata* as discussed under those species. Females have the pronotum subquadrate, without a discrete medial depression, the propodeum is posteriorly convex in lateral view, and the metanotum is sunken dorsally and forms a narrow, deep notch between the scutellum and propodeum.

Material examined.—(1512 males and 32 females); CHILE: Arauco: Contulmo (xii, ii), Pichinahuel (ii), Caramavida (i, ii), 20 km w Caramavida (i); Aysen: Lago Frío (i), 15 km s Las Juntas (xii), 16 km nw Cisnes Medio (xii, i), El Buchen (ii); Bio-Bio: El Abanico (xii); Cautín: Villarrica (x), 30 km ne Villarrica (i), Pucon (ix, xii), Temuco (i), La Selva w Temuco (xii), Volcan Villarrica (xii-ii), Cherquenco (i), Bellavista n shore Lago Villarrica (xii), 15 km ne Villarrica (ii); Chiloé: Cacao (xii), Ancud (xii), 22 km n Quellon (xii), Dalcahue (i); Curicó: El Coigual (x-i), Las Trancas (iii), Río Colorado (i), Cubillo Cordillera Curicó (i), El Buchen (ii); Linares: Estero Leiva (i); Llanquihue: 3 km e Casa Pangue (xi), Lago Chapo (xi); Malleco: 40 km w Curacautín (xii-ii), Cordillera Nahuelbuta (i), Termas de Río Blanco (i), Curacautín (ix-ii), Angol (xi), 12 km e Malacahuelo (xii), Laguna de Catren (xii). Las Raíces (xii, ii), Princesa 20 km w Curacautín (xii), 17 km w Angol (xii-ii), 30 km w Angol (ii), 40 km w Angol (xii-ii); Nuble: Chillán (xii, ii), Trancas se Recinto Shangri-La (xii), Las Cabras (xi, i), 60 km se Chillán (xii-ii), Recinto (xii), Las Trancas (i, ii), se Termas de Chillán (xii), 22 km ese Recinto (xii); Osorno: Puyhue (xii-ii), Pucatrihue (ii), Anticura (xi); Santiago: Santiago (iii); Talca: Alto de Vilches (x-i), El Radial (i); Valdivia: Chanchan (iii), Valdivia (xi, xii); ARGENTINA: Chubut: Puerto El Sagrario Lago Mendez (i), Cholila (ii), PN Los Alerces (xi, xii); Neuquén: Cerro Chapelco (xi), Lago Lacar 5 km e Hua-Hum (x, xi), Pucará (xii-iii), PN Lanín (x,

i, ii), PN Nahuel Huapi (xii-ii); Río Negro: El Bolsón (xii) El Tronador (ii), Bariloche (xi, xii), Lago Mascaró (xi), 11 km e Llao Llao (xii), Lago Nahuel Huapi Puerto Blest (xi), 4 km s Moreno (xi), Puerto Frías (xii), 114 km w Bariloche (xii).

Elaphroptera quadrilobata Genise and Kimsey,
new species
Figs. 10, 28, 50

Male.—(Holotype) Body length 13 mm; forewing 11 mm; clypeus subconical medially, apical rim with 4 lobes (Fig. 10); mandible apically bidentate, with small subbasal angle on inner margin, elbowed in lateral view; flagellomere I length 2.6 times breadth; flagellomere II 3.2 times as long as broad; scutellum broadly conical; sternum VII with sharp medial lobe and 2 rounded lateral ones; genital capsule (Fig. 50); gonocoxa sunken dorsomedially, with short closely appressed apical lobes, angulate sublateral lobes nearly touching each other; gonostylus slender, tapering abruptly near apical third, widest medially; digitus long lanceolate; cuspis flattened and appressed to aedeagus; aedeagus with large lateral winglike lobes at base of apical loop. Body black, except pale mark on vertex at top of each eye, posterior pronotal margin and tegula pale, pubescence long and pale; wings lightly brown stained.

Female.—Body length 7 mm; frons with small ovoid pit at apex of medial sulcus; pronotal disk subquadrate, elevated abruptly above collar; scutellum, pronotum and propodeum planar; propodeum with long dorsal surface, abruptly declivous posteriorly, posterior surface nearly flat; sternum V without posterolateral corners projecting; tergum VI rugose area widest dorsally, apical rim V-shaped (Fig. 28); sternum VI rim broadly V-shaped. Body reddish brown, paler on face between eye and antenna.

Diagnosis.—The most unusual feature of this species is the apically quadrilobate male clypeus, which lacks a ventral bevel. Although not all *Elaphroptera* have the male apical clypeal margin emarginate, none of the rest have medial lobes of this kind. Modifications of the male genitalia, including the aedeagus without dorsal or ventral lobes, the cuspis simple, gonocoxa dorsomedially

emarginate, and digitus large and foliaceous, suggest a relationship with species found in Peru and Bolivia, *cuzcoensis* and *boliviana*. Other diagnostic features of male *quadrilobata* are the simple, unbent mandibles, and long pale setae on the otherwise black body. Based on the subquadrate, undivided female pronotum *quadrilobata* females most closely resemble those of *nigripennis*, *scoliaefornis*, and *cuzcoensis*. However, this feature is probably of little phylogenetic value, as it is probably the primitive state. Other diagnostic features of female *quadrilobata* are the propodeum with a long dorsal surface and abruptly declivous posteriorly, and sternum and tergum VI both apically V-shaped.

Etymology.—The species name refers to the four-lobed male clypeus.

Types.—Holotype male: CHILE: Coquimbo Prov., Manquehua, s Punitaqui, 1-5 August 1960, L. E. Peña (DAVIS). Paratypes: 1 male, Aconcagua, Termas de Jahuel, near San Felipe, 16-19 October 1984, C. Porter and T. O'Neil (GAINESVILLE).

Elaphroptera sanguinicauda Durán-Moya
Figs. 11, 17, 51

**Elaphroptera sanguinicauda* Durán-Moya
1941:150. Holotype male; Chile (VIENNA).

Male.—Body length 15 mm; clypeus with sharp, noselike medial projection, acute in lateral view, apical margin projecting ventrally, medially truncate or slightly bilobate, deeply notched laterally, without ventral bevel (Figs. 11, 17); mandible slender, apically bidentate, with sharp subbasal tooth on inner margin, not particularly elbowed in lateral view; flagellomere I 2.2 times as long as broad, flagellomere II length 3 times breadth; scutellum broadly rounded; sternum VII apically trilobate; genital capsule (Fig. 51); gonocoxa not depressed dorsomedially, dorsoapically projecting and apical lobes slender and narrowly rounded apically; gonostylus small and somewhat narrowed medially, about 4 times as long as broad, with broadly rounded dorsal lobe; digitus broadly C-shaped; cuspis broad and flat with long tapering ventral and dorsal lobes extending on either side of aedeagus; aedeagus with digitate dorsal lobe before apical loop and widened ventral lobe. Body black with

apical 2 abdominal segments and legs red, pubescence silvery; wings lightly brown tinted.

Diagnosis.—The structure of the male mandibles, general clypeal shape and coloration indicate a close relationship between *erythrura*, *sanguinicauda* and *herbsti*. However, the structure of the genital capsule is very different from these species, more closely resembling that of *nigripennis*. Additionally, male *sanguinicauda* can be distinguished from them by having the clypeus apicolaterally notched and with a lip-like flap below the medial projection. The female is unknown.

Material examined.—(27 males) Chile: Coquimbo; Santiago: La Dormida to Tiltil (xi), Cerro Colorado near Renca (xi); Valparaíso: Las Viscachas (xii).

***Elaphroptera scoliaeformis* (Haliday)**

Figs. 29, 31, 52

**Myrmecodes scoliaeformis* Haliday 1836:327. Holotype female; Chile (LONDON).

**Myrmosa dimidiata* Haliday 1836:328. Syntype males; Chile (LONDON, OXFORD). Synonymized by Turner 1910b.

Elaphroptera dimidiata Guérin-Ménéville 1838:240. Holotype female; Chile (GENOA?). Synonymized by Dalla Torre 1897. Nec Haliday 1836.

Elaphroptera pallidipennis Guérin-Ménéville 1838:241. Holotype male; Chile (GENOA?). Synonymized by Dalla Torre, 1897.

Male.—Body length 23–30 mm; clypeus with small sharp noselike medial projection, apical margin broadly emarginate with narrow ventral bevel, lateral apical tooth acute; mandible apically bidentate, with small subbasal tooth on inner margin, strongly elbowed in lateral view; flagellomere I length 2.5 times breadth; flagellomere II 2.8 times as long as broad; scutellum rounded conical; sternum VII with sharp medial tooth, lobate laterally; genital capsule (Fig. 52): gonocoxa strongly produced dorsomedially into elongate and slender apical lobes; gonostylus long and slender narrowest at base, 5 times as long as broad, with strongly rounded dorsal lobe; cuspis large and flattened against aedeagus, digitus a slender digitate apical lobe;

aedeagus with large flattened dorsal and ventral lobes, and lateral lobes large and apically expanded, extending cuplike over cuspis. Head, thorax and legs black, abdomen red, except base of tergum I black; wing membrane dark brown; pubescence black.

Female.—Body length 16–18 mm; frons with medial sulcus; gena rounded ventrally; pronotal disk subquadrate, convex in lateral view, elevated above collar; propodeum without distinct dorsal surface, with thickened and rounded dorsal and lateral margin, sunken dorsomedially, posterior half convex (Fig. 31); tergum I with anterior brush of dense long setae; sternum V posterolateral corners unmodified; tergum VI rugose area twice as long as broad, tapering apically to short medial projection subtended by short even row of setae, deeply notched laterally (Fig. 29); sternum VI V-shaped posteriorly. Body dark brown to black with yellow maculae between eye and antenna.

Diagnosis.—This is the most commonly encountered thynnine species in the southern Andes. It is also the largest bodied *Elaphroptera* species. Males fly low over the ground in large numbers in some areas, searching for females. *E. scoliaeformis* does not appear to be closely related to any other species, although it superficially resembles *clypeicarinata* in size and coloration. The most distinctive features of male *scoliaeformis* are the all red abdomen, elbowed mandibles, clypeus conical medially with broad apical emargination, gonocoxa strongly projecting dorsally, and small, digitate digitus. Females are also generally larger-bodied, usually more than 1.5 cm long, than those of other species although smaller individuals do occur. They can be distinguished from other species by the the subquadrate relatively flat pronotal disk, propodeum with little or no dorsal surface, and declivity convex, and tergum VI narrowed and tapering apically.

Material examined.—(1445 males and 85): CHILE: Arauco: Contulmo (iii), Caramavida (ii), Pichinahuel (ii), Llicurá (xii), Manzanar (xii); Bio Bio: El Abanico (xii); Chiloe: Dalcahue (i), Chiloe (xii); Concepción: Salto de Laja (xii-i), Concepción (x, xii, i), 6 km s San Pedro (xii); Cautín: Villarrica (x-xii), 15 km ne Villarrica (xii-ii), 10 km ne Pucon (i), 21 km ne Pucon (xii-ii), 30 km ne Villarrica (i), 20 km e Temuco (i), Bellavista n shore Lago

Villarrica (xii), Lago Caburgua (i), La Selva w Temuco (xii), Chacamo w Temuco (i); Curicó: Las Trancas (iii), Cordillera Cubillo (i), Río Teno (xi), El Coigual (x-i), Cajón de Río Claro se Los Quenes (x), Río Colorado (i), Río Vergara (i), 6 km e Los Quenes (i), Buchen (i), Los Quenes Estero La Juala (i); Linares: Estero Leiva (i); Llanquihue: Maullín (ii), Petruhue (xi), 12 km s Los Muermos (xi), 3 km e Casa Pangue (xi), Lago Chapo (xi), Fresia (xi); Malleco: 17 km w Angol (xii-ii), Contulmo National Monument (xii-ii), 14 km e Malacahuelo (xii), Las Raíces (x-xii), La Fusta (xii), Angol (i), Victoria (xi-ii), 45 km w Angol (xii-ii), Termas de Río Blanco (i), Curacautín (ix-xii), 30 km w Angol (ii), 20 km w Curacautín (xii-ii); Maule: 15 km e Curanipe (i), Tregualemu w Cauquenes (xii); Nuble: Las Trancas (xii-ii), Recinto (xi, xii), 60 km se Chillán (xii-ii), Refugio Las Cabras (ii), 40 km e San Carlos (xii), 15 km e San Carlos (xii); Osorno: 20 km e Puyehue (i), Puyehue (xi-ii), Río Gol Gol (xi), 30 km w Purranque (i), Pucatrihue (ii), 8 km w Refugio la Picada (ii); Santiago: El Canelo (xi-xii), El Peumo (i), Guayacan (xii), La Pirámide (i), Macul (xii), El Armayan (x), Quebrada El Manzano (ii), San José de Maipo (x), Huelquen (xii), Santiago (x-xii), Río Colorado Maipo Canyon (x); Talca: El Radial (i), Alto Vilches (x-xii), 22 km n Talca (xii); Valdivia: 20 kms Valdivia (xi), Cudico (xi), Valdivia (x-ii), Chanchan (iii), Neltume (iii), Rinihue (ii), Enco (iii), Puerto Fui (iii), Corral (x), Bas. Chihuío (ii); Valparaíso: Zapallar (xii); ; ARGENTINA: Chubut: El Bolsón Lago Puelo (x), Parque Nac. Los Alerces (xi, xii), El Maitén (i); Neuquén: Pucará (xi-i), Lago Lacar (x), Parque Nacional Lanín (xi-ii), Parque Nac. Nahuel Huapi (xii-iii); Neuquén (iii); Río Negro: 14 km w Bariloche (xi, xii), 11 km e Llao Llao (xi), Llao Llao (xii), Bariloche (xi), El Bolsón (xi), 4 km s Puerto Moreno (xi), Lago Mascaridi (xi), Río Los Repollos (xi).

***Elaphroptera spatulata* Genise and Kimsey,**
new species

Figs. 12, 14, 20, 22, 53

Male.—(Holotype) Body length 13 mm; forewing length 11 mm; clypeus apically broadly emarginate, with large medial tooth dividing ventral bevel as well, lateral angle sharp (Figs. 12, 14);

mandible apically bidentate, with large ventral tooth and large swelling submedially on inner margin; flagellomere I length 2.3 times breadth; flagellomere II 2.7 times as long as broad; scutellum conical; sternum VII apically tridentate; genital capsule (Fig. 53): gonocoxa dorsomedially ending in two large rounded lobes, sunken between sharp submedial lobes; gonostylus less than twice as long as broad, broadest medially, strongly tapering apically; digitus foliaceous, inner margin strongly angulate near midline of gonocoxa; cuspis flattened, truncate apically, appressed to aedeagus; aedeagus with winglike lateral lobes before apical loop, and small ventral lobe. Head, thorax, legs and abdomen black, except pale spot near top of eye, posterior pronotal margin pale and abdominal segment VII red; pubescence erect and golden; wing membrane light amber colored.

Female.—Body length 9 mm; face with deep medial sulcus extending ventrally from small frontal pit; thorax (Figs. 20, 22): pronotal disk subtriangular with sharp, carinate medial projection and broadly rounded lateral lobes; propleuron ventrally flattened and necklike; scutellum bulging and laterally compressed; propodeum with tiny dorsal surface, posterior surface concave above midline, convex below; sternum V unmodified; tergum VI rugose area about as broad and long, broadly truncate apically; sternum VI with narrow broadly U-shaped apical rim. Body dark brown with pale spot on face between eye and antennal socket.

Diagnosis.—The odd, strongly angulate mandible in males of this species suggests a close relationship with *strandi*, as discussed under that species. Male *spatulata* can be immediately recognized by the strongly trilobate clypeal apex, gonocoxa dorsally with submedial lobes small and barely separated, and gonostylus short, wide medially and strongly tapering apically. Females have a subtriangular pronotal disk, which is level with the anterior collar medially, little or no dorsal propodeal surface, and ventrally convex propleura. Females also most closely resemble those of *strandi*, sharing similar pronotal and propodeal modifications.

Etymology.—The name *spatulata* refers to the peculiar male mandibles, which are ventrally broadened and shovel-like.

Types.—Holotype male: ARGENTINA: Tucumán, Tafí Viejo (BUENOS AIRES). Paratypes: 1 male and 1 female, same data as type; 1 male: Tucumán, Horco Molle, 24 April–9 May 1968, C. C. Porter (BUENOS AIRES, DAVIS).

***Elaphroptera strandi* Turner**

Figs. 13, 54

**Elaphroptera strandi* Turner 1910a:215. Lectotype male (desig. by Kimsey and Brown 1983); Peru: Marcapata (LONDON).

Male.—Body length 16–18 mm; clypeus with apical emargination extending dorsally two-thirds of the way through the clypeus, with rounded elongate lobe on either side, ventral bevel confined to middle of emargination (Fig. 13); mandible apically bidentate, with large subapical angle on outer margin, inner margin with large submedial projection; flagellomere I 2.2 times as long as broad; flagellomere II length 2.3 times breadth; scutellum rounded; sternum VII apically trilobate; genital capsule (Fig. 54); gonocoxa deeply sunken dorsomedially, with slender, medially constricted apical lobes, and adjacent large acute submedial lobes; gonostylus long and slender, about 4 times as long as broad, tapering apically, narrowed at base; digitus foliaceous; cuspis short and subtruncate, appressed to aedeagus; aedeagus with lateral transparent wing-like lobes before apical loop. Body black, pubescence pale, wings lightly brown stained.

Female.—Body length 8–10 mm; frons with narrow medial sulcus; pronotal disk curved laterally, elevated medially in broad ridge or hump; propodeum with horizontal dorsal surface about as long as scutum followed by concave slope ending in vertical declivity; sternum V without posterolateral projection or swelling; tergum VI broadly subovoid, posterior margin irregularly truncate with membranous edge; sternum VI apex deeply notched sublaterally, resulting in 3 apical truncate lobes. Body dark brown, paler on face between eye and antenna.

Diagnosis.—This species is most similar to *spatulata*, based on the large angle on the inner surface and second subapical angle on the outer surface of the male mandibles, gonocoxa

dorsomedially emarginate, digitus large, and foliaceous, and aedeagus without dorsal or ventral lobes. *E. strandi* can be distinguished from *spatulata* by the deeply emarginate and strongly lobate male clypeus, a feature unique in *Elaphroptera*, the gonocoxa dorsally with submedial lobes large and well separated, and the gonostylus slender and parallel-sided. Females also closely resemble those of *spatulata* as discussed under that species. They can be distinguished by the apicolaterally notched sternum VI, a feature not found in *spatulata*.

Material examined.—(233 males and 160 females): PERU: Marcapata, ARGENTINA: Salta: Cuesta Obispo (i–iii).

***Elaphroptera vulpina* (Klug)**

Figs. 19, 55

**Thynnus vulpina* Klug 1842:36. Lectotype male (desig. by Kimsey and Brown, 1993); Brazil: Porto Alegre (BERLIN).

Male.—Body length 15–17 mm; clypeus appearing conical in lateral view, apex deeply emarginate, apex of emargination strongly protruding, with sharp tooth on either side, ventral bevel large and subtriangular (Fig. 19); mandible apically bidentate with swelling or obtuse angle adjacent to subsidiary tooth, and small subbasal tooth on inner margin, elbowed in lateral view; flagellomere I length 2.2 times breadth; flagellomere II length 3 times breadth; forecoxa short and globular, ventrally with medial projection overhanging a concave area before apex; scutellum conical in lateral view; sternum VII trilobate; genital capsule (Fig. 55); gonocoxa dorsomedially depressed, with apicomedial lobes slender and basally constricted and sharply incised between large, flat sublateral lobes; gonostylus long and slender, at least 3.5 times as long as broad, tapering apically and slightly narrowed at base; digitus large and foliaceous; cuspis small and appressed to aedeagus; aedeagus with small sharp dorsal projection, rounded ventral lobes and truncate lateral winglike lobes before apical loop. Head, thorax, coxae and base of abdominal segment I black; mandible, small spot next to top of eye, clypeal apex, posterior pronotal

margin, tegula, legs beyond coxae and rest of abdomen red; pubescence long, erect and golden; wing membrane amber-colored.

Diagnosis.—The structural similarities between this species and *haematodes* have been discussed under *haematodes*. *E. vulpina* can be distinguished by the male clypeal margin projecting and acute in lateral view, not hooked at tip, and with an acute lateral tooth. Females are not known.

Material examined.—(9 males): BRAZIL: Santa Catarina: Nova Teutonia (ix, x, ii), Cruzeiro (xii), São Paulo: Cerro Negro (xii).

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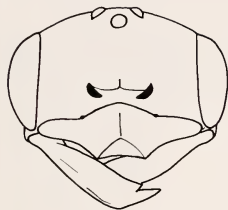
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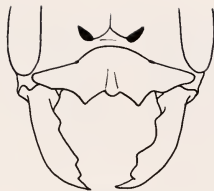
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Fig. 1. Distribution map of species of the genus *Elaphroptera* Guérin-Ménéville. Southern Andean species include: *arcuata*, *atra*, *clypeicarinata*, *erythrura*, *herbsti*, *hyalinipennis*, *intaminata*, *nigripennis*, *quadrilobata*, *sanguinicauda*, and *scoliaeformis*. The central Andean region, from southern Peru to northern Argentina includes the species: *boliviana*, *cuzcoensis*, *dorada*, *fuscata*, *spatulata* and *strandii*. Southern Brazilian species are: *haematodes*, *montifacies* and *vulpina*.



2. *boliviana*



3. *clypeicarinata*



4. *cuzcoensis*



5. *dorada*



6. *fusca*



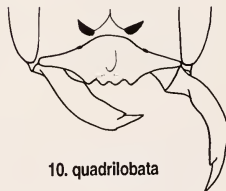
7. *haematodes*



8. *montifacies*



9. *nigripennis*



10. *quadrilobata*



11. *sanguinicauda*

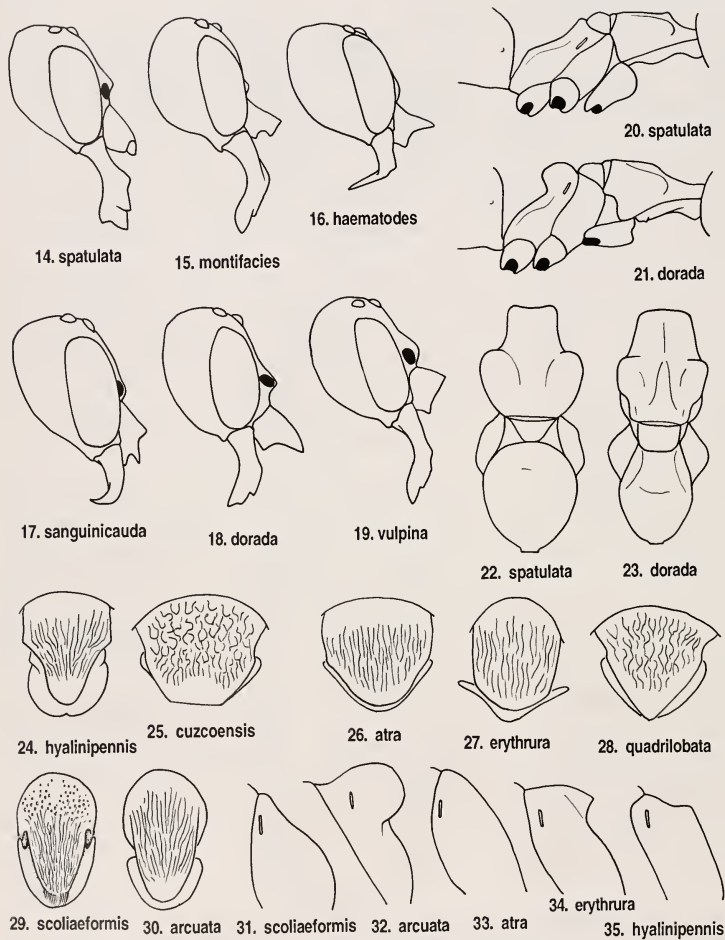


12. *spatulata*

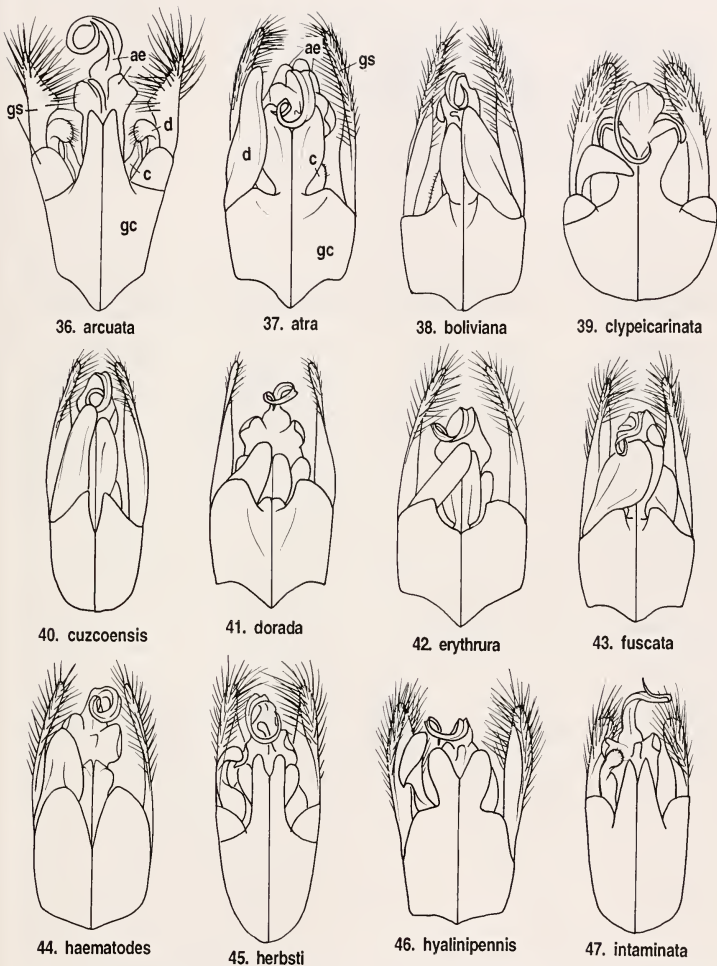


13. *strandi*

Figs. 2-13. Front view of male face. Figs. 3-13. Face with frons and vertex removed.



Figs. 14-19. Male head, lateral view. Figs. 20-21. Female thorax, lateral view. Figs. 22-23. Female thorax, dorsal view. Figs. 24-30. Posterior view of female apical abdominal tergum. Figs. 31-35. Female, propodeum, lateral view.



Figs. 36-47. Male genital capsule, dorsal view, with cuspis removed from one side. Abbreviations: ae = aedeagus, c = cuspis, d = digitus, gc = gonocoxa, gs = gonostylus.

48. *montifacies*49. *nigripennis*50. *quadrilobata*51. *sanguinicauda*52. *scoliaeformis*53. *spatulata*54. *strand*55. *vulpina*56. *intaminata*57. *arcuata*58. *boliviana*59. *fuscata*60. *hyalinipennis*61. *montifacies*

Figs. 48-55. Male genital capsule. Figs. 48-50, 52-54. Dorsal view, with cuspis removed from one side. Figs. 51, 55. Lateral view. 2. Dorsal view of genital capsule. Fig. 56. Aedeagus, lateral view. Figs. 57-61. Detail of gonostylus, lateral view. Abbreviations: ae = aedeagus, c = cuspis, d = digitus, gc = gonocoxa, gs = gonostylus.

The Nest, Prey, and Larva of *Entomosericus kaufmani* Radoszkowski (Hymenoptera: Sphecidae)

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Abstract.—This paper presents, for the first time, information on the nest architecture and prey of *Entomosericus kaufmani*, one of two species in a genus of sphecid wasps whose phylogenetic placement is problematic. Adult females dig nearly vertical burrows in the soil and provision them with immature and adult leafhoppers (Homoptera: Cicadellidae). The mature larva of *E. kaufmani* is also described for the first time, and the phylogenetic implications of this new information on nesting biology and larval morphology are discussed.

Entomosericus is a small genus of only two species, occurring in northwest Africa, southeast Europe, Turkey, and south-central Asia (Kazakhstan to Turkmenistan). Nothing was known about the life history of these wasps until the first author found a colony of *Entomosericus kaufmani* in south-eastern Kazakhstan in 1988. The wasps were nesting on a dry sandy-silt terrace of the Talas River that was covered with sparse vegetation (*Artemisia* spp., *Dodarcia orientalis* (L.), *Halimodendron holodendron* (Pall.) Voss., *Salsola* spp., etc.). The nests were 20 cm to 1 m apart. Wasps visited the flowers of *Euphorbia jaxartica* Prokh., *Pyrethrum* sp., and other plants. Males sat on *Dodarcia* and other plants near the nesting area, and rushed toward females emerging from nests or arriving with prey.

Four nests were excavated. The burrows, 3 to 4 mm in diameter and 11 to 15 cm in length, were almost vertical. An oval cell 6 to 8 mm in diameter was at the end of each burrow. There were two to four lateral galleries just above the terminal cell. Nests were left open during the provisioning period. Immature and adult leafhoppers (Homoptera: Cicadellidae) were used as prey, and carried in flight. Eight to eighteen prey were stored per cell. I.D. Mityaev provided the following determinations of prey: *Scorlupella montana* (Fieb.), *Platymetopius albus* (Lindb.), *Neoliturus*

opacipennis (Leth.), *Chandianus* sp., *Pseudophlepsius* sp., *Psammotettix* sp., *Macrolestes* sp., and *Eremophlepsius sexnotatus* (Kusn.).

DESCRIPTION OF LARVA

This description is based upon two apparently full grown specimens collected by the first author at the nest site described above. These specimens were cleared and mounted on a microscope slide, and subsequently examined by the second author with an Olympus BH-2 microscope with differential interference contrast optics. All measurements presented in this description are taken from these slide-mounted specimens.

Body. Mean length 10.3 mm (10.2, 10.4 mm), mean maximal width 3.35 mm (3.3, 3.4 mm). Thoracic and abdominal segments with large transverse swellings dorsally and well-defined pleural lobes laterally (Fig. 1). Integument densely covered with minute spinules (Fig. 2).

Spiracles. Ten pairs of spiracles present, all of equal size; spiracular atrium with a few scattered denticles that are barely perceptible at 400x magnification (Fig. 3), opening between atrium and subatrium lined with minute denticles but not with long, narrow spines. Outer surface of wall of atrium with subparallel, anastomosing ridges (closely resembling Fig. 5, Plate XVIII in Evans, 1959).

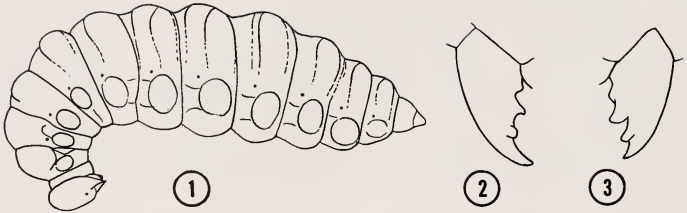


Figure 1-3. *Entomosericus kaufnani*. 1. General view of full grown larva. 2. Right mandible, anterior view. 3. Left mandible, anterior view.

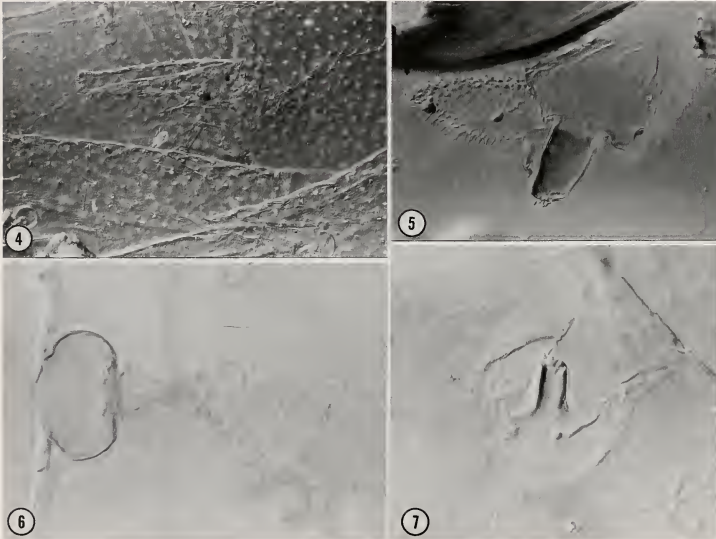


Figure 4-7. *Entomosericus kaufnani*. 4. Integument of mesothorax, showing spinules in various orientations, 100X. 5. Anterior surface of apex of left maxilla, showing palpus (long, dark, cylindrical structure with apical sensilla, galea (shorter cylindrical structure, with only the apex in focus), and lacinial surface, 200X. 6. Lateral view of spiracular atrium, subatrium, and trachea, 400+X. 7. Antenna, showing orbit and median papilla.

Head. Mean width 1.11 mm (1.12, 1.10 mm), mean height 1.05 mm (1.02, 1.08 mm). (Following Evans and Lin [1956], height is measured "from the top of the vertex (in full front view) to the apex of the clypeus".) Anterior surface of head almost entirely devoid of setae, integument smooth, not spinulose as on thorax and abdomen. Antenna (Fig. 4) with lightly tanned papilla in center of circular membranous antennal orbit. Papilla about 1.67 times as long as wide, apex of papilla bearing three stout, apically rounded sensilla.

Mouthparts. Apical margin of labrum broadly emarginate (Figs. 5, 8), armed with 12 stout setae along margin and about the same number of apparently pit-like submarginal sensilla (not clearly shown in the photomicrographs). Except for the most lateral sensillum on each side, these sensilla have the appearance of simple circles without an internal peg-like structure (cf. sensilla on epipharynx). Epipharynx densely spinulose laterally, spinules appressed and imbricate laterally, more erect along anterolateral margin of epipharynx (Fig. 8). Median portion of epipharynx with a narrow region devoid of sensilla or spinules, surrounded on each side by about 8 to 10 sensilla that appear to be circular pits with a central peg-like structure (Fig. 9). Hypopharynx a broad, convex lobe densely covered with sharp spinules (Figs. 5, 8). Mandibles heavily sclerotized and tanned, quadridentate (Figs. 10, 11), length about twice maximum width. Maxillae (Figs. 5, 6) with lacinial area directed strongly mesad, narrowly rounded apically, outer (ventral) surface densely clothed with sharply pointed spinules similar to those on hypopharynx and apical margin of epipharynx, inner (dorsal) surface with flattened papillae that appear to be associated with pitlike sensilla (Fig. 6). Inner face of stipes also papillose, but sensilla apparently not present. Maxillary palpus and galea lightly tanned, remaining parts of maxilla with unsclerotized and unpigmented cuticle. Length of maxillary palpus 3.18 times length of galea (accurate measurement is only possible on one maxilla of one specimen, but striking difference in length is obvious on both maxillae of both specimens). Maximum length of maxillary palpus 1.8 times its maximum width; apex of palpus with four or five stout, bristle-like or subconical sensilla. Maximum length of galea 1.2

times its maximum width; apex of galea with two stout, apically rounded sensilla. Apex of labium (Fig. 7) broadly rounded, bearing lightly tanned palpi laterally and a pair of apically pointed spinnerets (openings of salivary glands) mesally. Length of labial palpus about 1.6 times its width. Apex of labial palpus with at least 2 stout, subconical sensilla. Spinnerets conical, contiguous at base, sharply pointed at apex. Anterior surface of labium smooth, with about eight setae just dorsad of bases of palpi and spinnerets. Apicoventral surface of labium densely papillose, papillae longer and more erect than those on inner face of maxilla.

SYSTEMATICS

On the basis of adult characters, Bohart and Menke (1976) placed *Entomosericus* in its own subfamily because they could not confidently associate it with any other sphecoid group. The genus has a combination of adult morphological characters that suggest affinities with other subfamilies, particularly Alyssonini within the Nyssoninae and *Bothynostethus* within the Larrinae. They stated their preference for the hypothesis of a close relationship with *Bothynostethus*, and listed seven characters shared by *Bothynostethus* and *Entomosericus*, although they did not attempt to demonstrate that these are apomorphic similarities. They also listed eight characters in which *Entomosericus* differs from Larrinae (and Philanthinae).

Larval characters do not support the hypothesis of a close phylogenetic relationship between *Entomosericus* and Larrinae, if one accepts Evans' (1959) polarizations of larval characters. A major synapomorphy of all known larrine larvae is the subterminal, ventrally directed anus, and *Entomosericus* does not appear to have this character state. *Entomosericus* also possesses distinct antennal papillae, which are not present in larrine larvae. Evans argued that the presence of antennal papillae is apomorphic within the Sphecidae (although he noted that Michener (1953) considered the presence of antennal papillae to be plesiomorphic for bees). If antennal papillae are apomorphic, they indicate that *Entomosericus* could belong in a clade with Nyssoninae, Philanthinae, and Astatinae, although it should be noted that Evans (1959) hypoth-

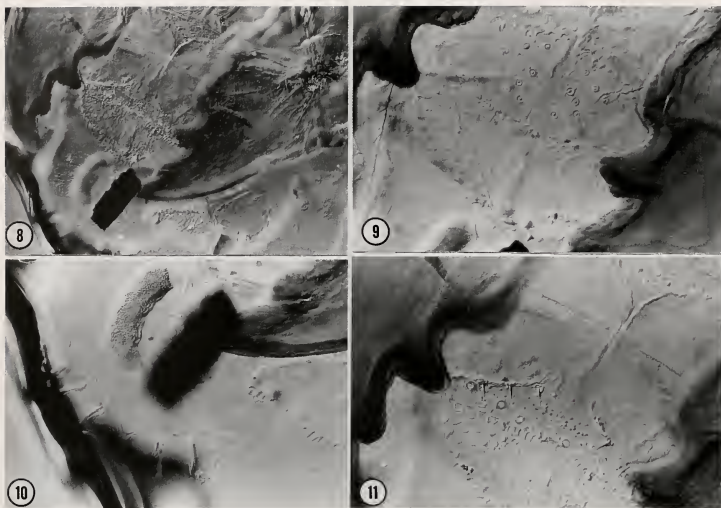


Figure 8-11. *Entomosericus kaufmani*. 8. Lower half of head in frontal view, plane of focus on labrum, clypeus, hypopharynx, and right mandible, 100X. 9. Median region of epipharynx, 200X. 10. Anterior surface of apex of labium, showing palpi (lateral cylindrical structures with apical sensilla) and spinnerets (paired median conical structures), 200X. 11. Apical margin of labrum and hypopharynx, 200X.

esized that antennal papillae have also arisen independently in two pemphredonine groups: Psenini, and *Spilomena* and *Ammoplannus* in the Pemphredonini. Another apparently apomorphic character state of *Entomosericus* is the densely spinulose integument of the thorax and abdomen (Evans, 1959). Neither the Nyssoninae nor the Larrinae have such an integument, but it does occur in Philanthinae and in the tribe Psenini of the Pemphredoninae. The mesally directed, apically pointed lacinial area of the maxilla of *Entomosericus* is unusual, but is at least superficially similar to the state described for certain psenine species such as *Pluto albifacies* and *Psen (Pseno)* sp. (Evans, 1959, Plate XVIII, Fig. 6 and 9). However, the inner face of the lacinial area in these psenine larvae does not appear from Evans' illustrations or verbal descriptions to be papillose, as in *Entomosericus*.

Larval characters do not seem to solve the riddle of the phylogenetic placement of *Entomosericus*, but information about larval morphology should certainly be considered in any future phylogenetic analysis.

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Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera)

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Abstract.—The development of ideas on the phylogeny of the aculeate Hymenoptera, especially Vespoidea and Chrysidoidea, since Brothers's 1975 and Carpenter's 1986 studies is reviewed. The results of their detailed analyses of aculeate higher taxa are re-evaluated in the light of new information and/or reinterpretations by subsequent workers. Almost all of their earlier results, including the relationships within the Chrysidoidea, the holophyly of Vespoidea (including Pompilidae), the sister-group relationship of Scoliidae (including Proscoliinae) and Vespidae, that of Sapygidae and Mutillidae (including Myrmosinae), and the composition of Bradynobaenidae are confirmed. The final preferred cladogram, using 219 variables and based on ground plans for all families of Chrysidoidea and Vespoidea and three taxa of Apoidea, indicates the following relationships (components of the superfamilies included within curly brackets): {Plumariidae + (Scolebythidae + ((Bethyloidae + Chrysididae) + (Sclerogibbidae + (Dryinidae + Embolemidae))))} + ({Heterogynaidae + (Sphecidae s.l. + Apidae s.l.)} + {Sierolomorphidae + (Tiphidae + (Pompilidae + (Sapygidae + Mutillidae)))} + (Rhopalosomatidae + (Bradynobaenidae + (Formicidae + (Scoliidae + Vespidae)))).

INTRODUCTION

Current ideas on the phylogeny of the aculeate Hymenoptera date from the publication of Brothers's (1975) paper, which was the first attempt to apply cladistic principles in an analysis of the entire group. Since the initial purpose of that study was merely the elucidation of the relationships of the components of the Mutillidae s.l., the paper had limitations in that the component taxa were dealt with in differing detail (analysing tribes in some taxa but lumping families presumed to comprise holophyletic groups elsewhere) and the sample of exemplars used to derive taxon ground plans was probably inadequate for some taxa. Although not all of the conclusions of that study have been accepted, it has fulfilled one of its major functions in stimulating further investigations of the relationships among the various higher taxa of aculeates. Carpenter's (1986) analysis of the families of Chrysidoidea being particularly significant. The present paper aims to survey the relevant literature which has appeared on the topic since 1974, to analyze new characters and interpretations presented therein, and to modify and amplify the data base of Brothers (1975) and re-analyze it in the light

of the new information. The final result is the best-supported cladogram available for the superfamilies of Aculeata and for the components of the Chrysidoidea and Vespoidea. We do not analyze the Apoidea in any detail since it is clearly a holophyletic group and analyses of some of its components are presented by Alexander (1990, 1992); that superfamily is in any case the group dealt with in least detail in the 1975 analysis.

Limits and names of the various taxa included in the Aculeata are sometimes problematic. Thus, Brothers's Bethyloidea and Sphecoidea should be Chrysidoidea and Apoidea respectively in terms of nomenclatural priority (Day 1977, Michener 1986), and the correct names are used below for these taxa even though other names may have been used by the authors of the papers under discussion. The abbreviations 's.l.' (*sensu lato*) and 's.s.' (*sensu stricto*) are used to indicate more and less inclusive concepts where confusion could result, e.g., Vespoidea s.l. is more or less the concept of Brothers (1975), whereas Vespoidea s.s. comprises only Vespidae s.l. (Masaridae + Eumenidae + Vespidae s.s.).

PREVIOUS STUDIES

In the following survey of papers on this topic, we generally deal with them in chronological order, starting in 1975 with Brothers's study which examined 25 taxa and 92 characters of Aculeata. The cladogram he obtained is reproduced here (Fig. 1) in the format generated by CLADOS (Nixon 1992) from Hennig86 version 1.5 (Farris 1988), the computer programs used for our new analyses, for easier comparison with them. The distribution of derived character states on the various internodes of the 1975 cladogram is also provided (Appendix 1A) to remedy a lack in the original paper; this is similar to the listing given by Wahl (1990) but with a few corrections. (Note that the distribution and numbering of variables shown in Fig. 1 results from one of our new analyses (see below) and is not the same as that used in the 1975 paper.) Major conclusions from the 1975 analysis were the establishment of the holophyletic nature of the Chrysidoidea, with Plumatidae as the sister taxon of the remaining chrysidoid families (exemplified by Scolioleptidae and an amalgam of other taxa); the recognition of the polyphyletic nature of the traditional superfamily Scolioidea, with placement of the Scolidae as the sister taxon of the Vespidae s.l. rather remote from the Tiphidae; the acceptance of only three superfamilies (Chrysidoidea, Vespoidea and Apoidea) instead of the traditional seven; inclusion of Pompilidae in Vespoidea rather than close to Apoidea; inclusion of Myrmecinae in Mutillidae rather than Tiphidae; and inclusion of Typhoctenidae, Chyphotidae, Apterogyninae and Bradynobaeninae in a single newly constituted family (Bradynobaenidae) rather than in Mutillidae and Tiphidae. Brothers (1976) further investigated the structure of the metapostnotum and second and third phragmata in various aculeates, finding corroboration for his earlier conclusions.

In 1977 Rasnitsyn described a new subfamily of Scolidae based on a monotypic genus, *Proscolia* Rasnitsyn, which he considered indicated that "the ancestor of the family was at least as primitive as the Anthoboscinae (Tiphidae)", and thus probably most closely related to that taxon. Such a conclusion does not necessarily follow, however, since it is based on shared plesiomorphies.

Over three years, Saini & Dhillon investigated various modifications of the metatibial spurs (1978), mouthparts (1979a, b) and metathorax (1980) in 22 varied families of Hymenoptera. Single and often relatively derived representatives were apparently used for each family, so that the studies were very limited, providing no information on intrafamilial variation. Furthermore, there was no differentiation between plesiomorphies and apomorphies, invalidating their conclusions. On the basis of number and development of the metatibial spurs, they linked Mutillidae and Formicidae (including their Dorylidae) in one line, and Chrysididae, Scolidae, Sphecidae, Vespidae s.s., Eumenidae, Pompilidae and Apoidea s.s. in another. Looking at the mouthparts, they identified two lines of modification (in the maxillae involving the relative sizes of the galea and lacinia and in the labia the relative development of glossa and paraglossa), the first leading from Ichneumonidae to Chrysididae, Mutillidae and Formicidae, and the other from Chalcidoidea to Scolidae, Sphecidae, Vespidae s.s., Pompilidae, Eumenidae and Apoidea s.s. Their account of modifications of the metapleuron and metapostnotum could be interpreted to indicate close relationships between Chrysididae, Scolidae and Sphecidae, a lineage including Vespidae s.s., Eumenidae, Formicidae and Apoidea s.s., and distinctness of the Pompilidae. They disagreed with Brothers's (1975, 1976) interpretation of the origin of the 'propodeal triangle' (as an expanded metapostnotum) in Apoidea s.l.

Königsmann (1978), in that part of his survey of hymenopteran phylogeny covering the Aculeata, based his treatment to a great extent on Brothers's (1975) analysis but indicated large areas of uncertainty (Fig. 2), usually where he felt that the characters given by Brothers in support of particular internodes were weak or homoplastic. He placed Sclerogibbidae as the sister group of all other aculeates (on the basis of the multisegmented antennae and apparent lack of synapomorphies with any particular aculeate group), excluding it from the Chrysidoidea, but otherwise accepted the division of the aculeates into three holophyletic groups. He analyzed the remaining taxa within the Chrysidoidea in greater detail than Brothers had, and suggested a sister-group relationship between

Plumariidae and Scolebythidae (based on the common reduction of the pronotal collar), between Embolemidae and Dryinidae (based on the 10-segmented antennae and single mesotibial spur in both) and between Chrysididae and Cleptidae (based on integumental sculpture, wing venation, form of the ovipositor and possibly the lack of articulation and sensillar fields between the first and second metasomal segments) but could not resolve the relationships among these pairs of taxa or Bethyidae and Loboscelidiidae, the other two taxa he included. Within the vespoid group he accepted a sister-group relationship between Scoliidae and Vespidae, rejected Scolioidea as polyphyletic, accepted a sister-group relationship of Pompilidae and Rhopalosomatidae, was uncertain of the position of Sierolomorphidae, and used more traditional superfamily names but left many taxa unassigned to superfamily. His treatment did not aim to be an original cladistic analysis of all characters for all taxa, but instead relied almost exclusively on data published by other workers; it is thus limited in providing new interpretations, but is useful in explicitly indicating the weakest points in Brothers's analysis.

Walther (1979) examined the types and arrangement of antennal sensilla of 25 species of aculeates in 12 higher taxa. He confirmed the 'monophyly' of Formicoidea (based on a single representative!), Pompiloidea (five Pompilidae only), Vespoidea s.s. (five Vespidae and Eumenidae) and Apoidea s.s. (three Andrenidae and Apidae) and found no evidence for holophyly of Scolioidea (11 species in 8 taxa). He confirmed a close relationship between Mutillidae (exemplified by three of the most derived species in that taxon) and female Myrmosinae, found evidence to link Anthoboscinae and Tiphinae, but found no characters linking Scoliidae and Vespidae or Myzininae and Methochinae, and rejected any close relationships between Formicoidea and Anthoboscinae or Methochinae (relationships which had also been rejected by Brothers 1975). His study was very limited, however, in that he considered a single character complex to the exclusion of all others, his sample for each taxon was exceedingly small (often only one), and he seems often to have used inappropriate exemplar species (highly derived ones). He presented no simple

coding of characters, so that his information cannot easily be included in any new cladistic analysis.

In his analysis of the evolution of the Hymenoptera, Rasnitsyn (1980) reinterpreted some of Brothers's (1975) characters and added a few new characters. In the Aculeata (his Vespomorpha; ignoring taxa known only from fossils, which were not considered by Brothers), he recognized the Chrysidioidea as a holophyletic group (including Sclerogibbidae), but split Brothers's Vespoidea into four superfamilies with Pompiloidea as the sister-group of Apoidea s.l. In the Chrysidioidea, he included Cleptinae and Loboscelidiinae in Chrysididae, rejected a close relationship between Embolemidae and Dryinidae (considering their similarities to be homoplastic), and postulated a sister-group relationship between Sclerogibbidae and Dryinidae. Although his figure (Fig. 3a) shows Scolebythidae as the sister taxon of (Embolemidae + (Bethyidae + Chrysididae)), this contradicts his discussion in which he stated that he preferred not to draw conclusions as to which of Plumariidae and Scolebythidae diverged the earlier from the stem leading to the remaining Chrysidioidea (implying a trichotomy as shown in Fig. 3b). His Scolioidea is a paraphyletic group giving rise to Formicoidea and Vespoidea s.s., and with Mutillidae remote from Sapygidae, and Scoliidae the sister-group of Tiphidae + Mutillidae. In his discussion, Rasnitsyn implied that Tiphidae is paraphyletic, with both Scoliidae and Mutillidae independently derived from within it. Although his figure left Bradynobaenidae floating within the Scolioidea, his discussion indicates that he considered it an early offshoot of the larger scoliod clade, but he could not decide which of Sapygidae and Bradynobaenidae had diverged first; this is shown as a trichotomy in our version of his phylogeny (Fig. 3b). Although he used the concept of synapomorphy, at least in part, in deriving his phylogeny, he did not do a general analysis considering all states for all characters over all taxa. He was also often not explicit in his definitions of the various states of characters, so that it is sometimes difficult to be certain of the significance to be placed on various features. In many cases his interpretations were very heavily influenced by, if not entirely based on, his impressions of features in

fossils, which were allocated to their extant taxa and used to polarize his characters. There seems to have been a general application of the principle that states seen in older fossils are necessarily more primitive than states in more recent fossils or modern species. Such an assumption cannot be justified since a plesiomorphic state can persist in one lineage long after an apomorphic state of the same character has arisen in a related lineage, and the fossil record is far too fragmentary to resolve such situations. In order to estimate how well Rasnitsyn's (1980) phylogeny is supported by the characters he cited, we did an analysis based on as many characters (38) and states as we could extract with reasonable certainty from his account, using his interpretations but correcting two or three straightforward errors. These were coded using nonredundant linear coding (O'Grady & Deets 1987) (Appendix II; Table I) and analyzed using Hennig86 for the modern taxa. The analysis produced three equally most parsimonious unweighted cladograms, with fewer steps than implied by his trees (Figs. 3a, b) for those characters used by us (lengths 94 versus 115 and 116). The strict consensus tree (Fig. 4) is considerably different from that given in his paper. The major differences are that Pompiloidea is now the sister-group of the remaining Vespoidea, Mutillidae and Sapygidae are sister groups, and Scolioidea is the sister-group of Vespidae + Formicidae. In many respects this tree is more similar to that of Brothers (1975) than Rasnitsyn's tree(s). We thus conclude that Rasnitsyn's (1980) treatment is highly subjective and that the tree he presented is not the one which explains his own data most efficiently.

Day, Else & Morgan (1981) provided a detailed analysis of *Proscolia*, pointing out that it lacks various of the putative synapomorphies, such as reniform eyes, dorsally produced clypeus and elongated ligula, previously used to establish the sister-group relationship of Scolioidea and Vespidae. They made no detailed analysis of the effect of making the necessary changes in ground-plan states on the relationship between these families, but suggested that they were unlikely to affect it significantly, and rejected Rasnitsyn's (1977) suggestion that the characters of *Proscolia* indicate a close relationship with Anthoboscinae (Tiphidae).

The relationships within the Vespoidea s.s. were examined in detail by Carpenter (1981). He applied a numerical cladistic analysis to 50 varied characters and concluded that a single family (rather than three) should be recognized to include six subfamilies. In general he followed Brothers's (1975) interpretations of character state changes where he used similar characters, but the study was limited to the relationships within a group considered as a single final taxon by Brothers, so that any differences of interpretation are of limited general applicability.

Osten (1982) investigated the structure and musculature of the head and mouthparts in 48 species of Hymenoptera, with the emphasis on 'Scolioidea'. He found that the separation of mandibular and oral cavities by a cuticular bridge, previously cited as a defining character of Scolioidea by Börner (1919), for example, is very variable within that grouping, even differing between the sexes of a single species of scoliid (present in female but entirely absent in male), and thus invalid. He agreed with Brothers (1975) in rejecting Scolioidea as polyphyletic, but saw a close relationship between Scoliidae and 'Myzinidae', and between Mutillidae and 'Tiphidae' s.s. (*Tiphia* Fabricius). His conclusions were based entirely on a restricted number of characters and an inadequate sample of exemplars (these often being some of the most highly derived members of their taxa), however.

In 1984 Day clarified the position of *Heterogyna* Nagy, a genus which Brothers (1974, 1975) had tentatively placed in the Plumariidae (Chrysidoidea), based on the rather inadequate description and figures available to him. Day showed convincingly that this genus is an aberrant member of the Sphecidae s.l., for which he recognized a separate subfamily. Argaman (1985) reviewed the group (as a distinct family), and suggested a closer relationship with the Chrysidoidea, and Embolemidae in particular, but his ideas were mainly based on a somewhat confused mixture of shared plesiomorphies without any critical analysis of apomorphies. The correct name for this taxon was the subject of a ruling by the International Commission for Zoological Nomenclature (1987), which specified the stem to be '*Heterogyna*-' (to prevent

confusion with family-group names based on the lepidopteran genus *Heterogynis* Rambur).

Walther (1984) extended his examination of antennal sensilla in ants and proposed "a close phylogenetic relationship between the Formicoidea and the Scolioidea including the Scoliidæ". Unfortunately, this paper is merely an abstract, and no further details or justifications have been published.

Gibson (1985) carried out a detailed examination of various structures of the pro- and mesothorax, especially in Parasitica, and most of this study is irrelevant in the context of aculeate phylogeny. However, he did show that the close association of the pro- and mesothorax in the Scoliidæ and Vespidae must have been independently derived, rather than being a synapomorphy as Brothers (1975: Character 19) had postulated, but this did not invalidate the idea that the different forms of the prepectus in these taxa may have been derived from a common relatively derived condition (Brothers 1975: Character 29). The postulated sister-group relationship of these two taxa was thus weakened but not disproved.

The next major paper is that of Carpenter (1986) in which he analyzed the relationships of the families of Chrysidoidea. This is a detailed cladistic study based on 22 characters or character complexes, and including extensive analysis of previous interpretations of these characters and/or taxa, especially those of Rasnitsyn (1980). His cladogram (Fig. 5) is well-supported since most internodes have at least one unique synapomorphy. He unfortunately did not present a data matrix or explicit explanations of the codings of his characters, but he did list the inferred apomorphies for all nodes (components) and terminal taxa (terms). His analysis supported the traditional views of sister-group relationships between Chrysidae and Bethyidae and between Embolemidae and Dryinidae, placed Sclerogibbidae unequivocally and confirmed the inclusion of Plumariidae and the branching sequence of Plumariidae then Scolebythidae and the remaining Chrysidoidea, as suggested by Brothers (1975).

In his 1987 revision of *Bradynobaenus* Spinola, Genise suggested different ranks for the higher taxa of aculeates "in order to diminish the differences

between the classification of Hymenoptera Aculeata proposed by Brothers and the classical one" and to facilitate the construction of keys. Genise accepted Brothers's (1975) analysis as being the best and most objective then available, and merely modified his classification by raising the ranks of almost all higher taxa by one level. So, for example, the three superfamilies became informal groups with '-formes' endings and included 11 superfamilies. This necessitated the proposition of four new superfamilies, Sierolomorpoidea (Sierolomorphidae only), Tiphioidea (Anthoboscidae, Thynnidae, Myzinidae, Tiphidae s.s., Brachycistidae, Methochidae), Bradynobaenoidea (Chyphotidae, Typhoctidae, Apterogynidae, Bradynobaenidae s.s.) and Mutilloidea (Mutillidae, Sapygidae), and restriction of the Scolioidea to include Scoliidæ only. The scheme thus ended up as being more different from the classical arrangement than was Brothers's.

Schönitzer & Lawitzky (1987) studied the antenna cleaner by scanning electron and light microscopy in Formicidae (seven subfamilies), Mutillidae (four subfamilies) and Tiphidae (four subfamilies), by light microscopy alone in single or a few species each representing Bethyidae, Chrysididae, Bradynobaenidae, Eumenidae, Vespidae, Masaridae, Scoliidæ, Pompilidae and Sapygidae, and also consulted descriptions and published figures of a few other taxa. They related their findings to Königsman's (1978) phylogeny, and found some support for the holophyly of Formicidae, of (Sapygidae + Mutillidae) (although they indicated that the antenna cleaner in Myrmosinae is more similar to that in some Tiphidae), and of the four subfamilies of Tiphidae for which they had data. As the authors themselves admitted, too few characters (and too few representatives) were involved for them to draw any further conclusions.

The relationships of *Proscolia* were again examined by Osten (1988). He compared various morphological structures, particularly the mouthparts, across 27 species, representing about 13 taxa at the subfamily level or above, in Scoliidæ, Tiphidae (including Bradynobaeninae and Myrmosinae!), Mutillidae and Sapygidae. His cladogram of the 'Scolioidea', based on a few characters of the head and mouthparts only, indicated the

Tiphiidae s.l. as extensively paraphyletic, giving rise separately to Mutillidae, Scoliidae and *Proscolia* (sister taxon of Anthoboscinae and remote from the Scoliidae) but not to Myrmosinae or Sapygidae. These results must be evaluated with the realization that they are based on a very limited data set in terms of number of exemplars, number of higher taxa and number of characters used, and exclude such classical characters used to associate *Proscolia* and Scoliidae as the tripartite propodeum, striolate wing membrane and widely separated meso- and metacoxae.

Johnson (1988) examined the mesocoxal articulations in a wide but unspecified variety of hymenopterons, and dissected the extrinsic musculature in a broad selection, including 27 species in 14 families of Aculeata. He obtained little critical information from the limited number of characters involved, but confirmed the holophyly of Chrysidoidea and of each of the three families Mutillidae, Bradynobaenidae and Formicidae, using the cladograms of Brothers (1975) and Carpenter (1986). Since he did not list all the taxa examined, it is difficult to evaluate the general validity of his results, however.

Also in 1988, Rasnitsyn produced an English summary of his ideas, some of which had changed since his 1980 paper. His phylogeny of the aculeates ('Vespomorpha') differs slightly from the previous one, in that the Scoliidae are more basal in the Chrysidoidea, and the sequence of branches involving Sierolomorphidae, Falsiformicidae, Formicoidea and Vespoidea s.s. is different. In the text he indicated that the position of Bradynobaenidae was still obscure (referring to his 1980 paper for details), but now suggested common ancestry either with (Mutillidae + Tiphiidae) (his node 104) or with the clade including Sierolomorphidae (node 108); we have compromised and placed Bradynobaenidae as forming a trichotomy with both major branches involved (Fig. 6). As with his 1980 scheme, subjection of Rasnitsyn's own characters and states for the modern taxa (Appendix III; Table II) to a cladistic analysis using Hennig86, produces results which differ from his in many respects, and differ slightly from those produced by a similar treatment of his 1980 data (Fig. 4). Exact analysis produced six

equally parsimonious cladograms, the strict consensus of which is shown in Fig. 7a, and successive approximations character weighting produced two cladograms (strict consensus shown in Fig. 7b, resolving an additional taxon in Chrysidoidea). Major differences between Figs. 6 and 7 are the holophyly of the Vespoidea s.l. (including Pompilidae and Rhopalosomatidae), the unresolved relationships amongst the components of the 'Scoliidea' and the Formicidae-Vespidae, and the sister-group relationship of Mutillidae and Sapygidae in Fig. 7. The major differences between the earlier and later reanalyses are the positions of Formicidae, Scoliidae and Vespidae and the degree of resolution of the 'Scoliidea'. The same problems and limitations of methodology and philosophy apply to the 1988 paper as to that of 1980 (Carpenter, 1990a). Rasnitsyn (1988) made explicit statements that he preferred searching for new characters and re-evaluation of the reliability of the evidence to criteria such as parsimony in dealing with homoplasy, and that he disagreed with 'cladistics' ('phylogenetic systematics') in so far as the derivation of classifications is concerned, preferring to accept ancestral paraphyletic groups as valid taxa, which explains some of the anomalies. Regardless of the merits of those viewpoints as stated in such broad terms, parsimony cannot legitimately be rejected out of hand, especially when the differences between the lengths of the trees being compared are as great as here (131 versus 118 for Figs. 6 and 7a respectively).

Day (1988), in a general account of the British Pompilidae, rejected some of Brothers's (1975) supposed synapomorphies of Pompilidae and Rhopalosomatidae, stating that the fine structure of the hindleg cleaning apparatus is very different in the two (something about which we are not convinced after reexamination), that the common loss of the second abscissa of vein 1A in the hindwing ignores the presence of a claval lobe in Rhopalosomatidae (but these are surely different characters); and that the basal hamuli in Rhopalosomatidae are more like those of the primitive Xyelidae (which could be the result of subsequent reduction in the ancestor of Pompilidae). Instead, Day cited several features of Rhopalosomatidae which "parallel those of the vespids (*s. str.*)

branch", including the shape of the eyes, formation of a trochantellus (although this is probably a plesiomorphy, and is weakly present in some Pompilidae), coadaptation of the pronotum and mesothorax, form of propodeal to metasomal articulation, and articulation between first and second metasomal segments. Many of these characters have relatively more plesiomorphic states (often fairly similar to those in Pompilidae) in the brachypterous genus *Olixon* Cameron, however, and these could represent the ground-plan states for Rhopalosomatidae. In addition, Day questioned Brothers's (1975) interpretation of the ground-plan state for the metapleuron in Pompilidae (another putative synapomorphy with Rhopalosomatidae); our re-examination has led to extensive reinterpretation of this character (see new analyses below). Day came to no firm conclusions, but retained Pompilidae as an early offshoot of the vespid stock although probably not close to Rhopalosomatidae.

In a comprehensive general treatment of the British Hymenoptera, Gauld & Bolton (1988) followed Brothers's (1975) classification of the Aculeata (except that they reduced Spheciformes and Apiformes to a single family each), but unfortunately redrew his impressionistic tree of the relationships of the chrysidoid families in a formal manner instead of using the critically derived cladogram produced by Carpenter (1986). They stated that the Vespoidea was probably paraphyletic and suggested that the Pompilidae might have to be distinguished as a separate superfamily, without giving any evidence to support these ideas.

In a series of papers starting in 1987, Piek and his co-authors (Piek 1987, Piek et al. 1989, Piek 1989, Piek 1990) related their discoveries of novel components (kinins) in the venoms of various aculeates to Brothers's (1975) phylogeny, suggesting, in a stepwise fashion, how it should be modified to take their results into account. These papers are a particularly clear example of misguided attempts to invalidate a phylogeny based on numerous characters and taxa by consideration of only one or a few new characters which have been investigated in only a small number of taxa and apparently without taking the concepts of ground-plan analysis into account. The last tree proposed (Piek 1990) grouped

Mutillidae (based on 3 species in 2 derived subfamilies), Formicidae (6 species in 2 subfamilies), Tiphidae (2 species in 2 derived subfamilies), Scoliididae (3 species) and Vespidae s.s. (12 species) on the basis of the presence of kinins in their venoms (although these were not found in 2 of the 3 mutillids!). There is still insufficient information for the incorporation of this character into any general analysis of the Aculeata.

Kimsey (1991) re-evaluated the status and limits of the subfamilies of Tiphidae delimited by Brothers (1975), and came to the conclusion, based on a cladistic analysis of 19 characters, that his Thynninae should be subdivided, with a relatively more primitive component (Diamminae) falling in the cladogram in the same position as Brothers's Thynninae (not surprising since *Diamma* Westwood was used as the main representative when he derived the ground plan for his Thynninae), and the other component falling as the sister-group of Myzininae. Her cladogram is identical to that presented by Brothers in all other respects. Kimsey's interpretations of some characters are questionable, however, and she sometimes did not clearly distinguish between the two sexes. Thus, enlargement of the ocelli in males is not universal in Brachycistidinae since species of *Brachycistellus* Baker and some *Quemaya* Pate have small ocelli, are black in colour and may even be diurnal (Wasbauer, 1968). Not all male Myzininae have emarginate eyes (simple in *Pterombrus* Smith), so that this feature is probably not part of the ground-plan of that subfamily. The differences between the frontal lobes of Diamminae and some Thynninae are far slighter than indicated by Kimsey; in these there is merely a frontal swelling which may be associated with a slight expansion of the dorsal rim of the socket itself, not very different from the condition in many Anthoboscinae; some male Methochinae (e.g. species from North America and Trinidad examined by DJB) have even less development of frontal lobes. The pronotum is not universally vertical in Brachycistidinae; there is a short but distinct dorsal surface in *Quemaya* at least, although the pronotum is strongly concave posteriorly. Not all Tiphinae have only a single mesotibial spur; there are two in both sexes of *Paratiphia* Sichel at least. It is difficult to under-

stand how closed metacoxal cavities could be part of the ground plan of Thynninae when *Aelurus nigrofasciatus* Smith is illustrated as having distinctly open cavities; Kimsey gives no explanation or justification for her conclusion which is contradicted by her later study of some Thynninae (Kimsey 1992). Although most female Thynninae certainly have the metasomal apex considerably modified, this is not always the case (*Aelurus* Klug (Kimsey 1992), *Elaphroptera* Guérin and some unidentified Australian species examined by DJB have it similar to many other tiphiids) and so cannot be part of their ground plan. A bilobate eighth tergum is not universally present in male Myzininae; at least one *Pterombrus* sp. (from Trinidad) has it simple. In the absence of further justification, we are not convinced that the ground-plan state of the male hypopygium (metasomal sternum VIII) in the Thynninae is unciform; some thynnines (e.g., *Aelurus* (Kimsey 1992) have simple hypopygia (although not identical to those in Anthoboscinae) which is the groundplan condition for the family, most have a wide variety of modifications (including some with a single strong upcurved process but different in formation from the superficially similar condition in Myzininae and Methochinae), and apparently only one genus (not named by Kimsey) has it unciform. Kimsey's treatment of the form of the hypopygium as two separate characters, thus coding Thynninae as simultaneously unciform and "elaborately lobate and sculptured", is also illogical. Furthermore, we are not convinced of the validity of the proposed synapomorphy of volsellar elaboration in Myzininae and Thynninae: the digitus and cuspis are somewhat elaborate and well articulated in at least some tiphiines such as *Paratiphia* and Kimsey (1992) even stated that various thynnine genera have the same condition as considered primitive for the family.

Quicke, Fitton & Ingram (1992) examined ovipositor structure, with particular reference to the valvilli, in a wide variety of Hymenoptera, with particular emphasis on Ichneumonoidea but also including Chrysidoidea (6 species in 4 families), Vespoidea (24 species in 7 families, but mainly ants) and Apoidea (9 species, mainly various bees). Their findings confirmed those of Oeser (1961) and Brothers (1975) and provided additional justifica-

tion for considering the presence of valvilli to be ancestral in Aculeata.

Also in 1992, Quicke, Ingram, Baillie & Gaitens examined sperm structure in a variety of Hymenoptera, including about 20 species of Aculeata in the following taxa: Chrysidoidea: Dryinidae; Apoidea: Andreninae, Anthophorinae, Megachilinae, Apinae, Xylocopinae, Astatinae, Larrinae, Nyssoninae, Pemphredoninae, Sphecinae; Vespoidea: Eumeninae, Vespinae, Polistinae, Pompilidae, Formicidae. Although some interesting results were obtained which indicated the potential usefulness of such studies for hymenopteron systematics, the data are still insufficient to be incorporated in any re-analysis of the aculeates as a whole.

NEW ANALYSES

For our new studies, various sets of data were subjected to analysis using different options of Hennig86 (Farris 1988) to obtain the most parsimonious cladograms and strict consensus trees with and without the application of successive approximations character weighting. Polarization of characters was based on outgroup comparison, using a wide variety of species of Ichneumonoidea and Symphyta, and the trees were rooted by the addition of an ancestral outgroup with all variables coded 0. Character weighting was applied to give some indication of which cladogram derived without weighting might be preferred. Tree plots and optimizations of placements of derived states were done using Clados (Nixon 1992) both using the accelerated transformation option (which applies the criteria of Farris (1970), maximizing reversals and minimizing parallelisms) and also using the delayed transformation option (which applies the criteria of Swofford & Maddison (1987), maximizing parallelisms and minimizing reversals). In all cases, variables for which values are unknown or inapplicable for some taxa were 'squeezed' (Nixon 1992) so that state changes were placed as far from the base of the tree as possible (distal to the points of origin of taxa for which the values are missing) to avoid the indication of apparent synapomorphies based only on the putative sharing of missing states (Platnick, Griswold & Coddington 1991). The plots and appendices giving state placements are

based on those produced by accelerated transformation (the optimization preferred on a theoretical basis by de Pinna (1991)), except that variables for which reversals are considered unlikely on evolutionary grounds (such as Dollo's law), are placed according to delayed transformation. Manual analysis of such optimizations on consensus trees based on successive weighting sometimes showed that different placements could further reduce the number of reversals without increasing the number of steps; this often lead to a resolution of tree topology and thus an indication of the fully dichotomous cladogram (from the set of underlying cladograms) to be preferred. In all cases, such a preferred cladogram was found to be identical to one from the initial set of cladograms derived without the application of character weighting. Choice of cladogram was also influenced by comparison with the results of the other analyses. The appropriate optimizations of variables on the preferred unweighted cladogram were then carried out; for a few 'irreversible' variables, manual modification of delayed transformation placements enabled reversals to be eliminated without increasing the number of steps.

The first attempt to subject Brothers's (1975) phylogeny to a critical analysis using modern techniques, particularly efficient computer derivation using Hennig86, was done by Carpenter (1990b). The cladogram which was presented, derived from Brothers's data as far as Carpenter was able to reconstruct them from the original paper and using nonredundant linear coding, agrees closely with Brothers's tree, although there are a few differences. That treatment was a preliminary one and unfortunately included a few errors, and also scored sexually dimorphic characters as missing. The data base was re-evaluated through consultation between both of us and an improved version, with a few changes to scoring and coding, was subjected to analysis. A list of the 162 variables, showing their derivation from the original 92 characters, is given in Appendix IV, and the data matrix appears as Table III. (Note that here (and in subsequent analyses) the variables refer to the conditions in the relatively least modified forms (e.g., to macropterous individuals where the taxon also contains brachypterous or apterous ones), unless there is a

statement to the contrary.) Brothers's analysis had considered differential expression of character states in the two sexes in some detail, and this was particularly significant in his estimates of amounts of phenotypic divergence. In the present re-evaluation, however, for a taxon where there is sexual dimorphism in the expression of character states, such that for a particular taxon only one sex has a relatively apomorphic state which occurs elsewhere in the other or both sexes (whether in an entire taxon or only part of a taxon), the relatively plesiomorphic state was scored (in analogy with ground-plan analysis); if the relatively apomorphic state does not occur elsewhere in the other sex, however, then the relatively apomorphic state itself was scored. This simplification is unlikely to have any material effect on the estimates of the branching pattern.

Two sets of analyses were run, one using only those characters identified by Brothers (1975) as the most significant in deriving his phylogeny, and the other using all characters. Interestingly, the results using all characters were consistently more similar to the 1975 tree than those based on the restricted character set. Since there is no good reason to exclude any characters, the restricted data set was discarded and further analyses were based on the full set of 162 characters. When no weighting was used, eight equally parsimonious cladograms resulted. The strict consensus tree appears in Fig. 8a. The application of successive approximations character weighting produced two cladograms, each identical to one of the original eight. One of these two cladograms is preferred (Fig. 8b), both on the basis of manual optimization of states on the consensus tree (see above; Variables 72, 83 and 95), and also because this is the one most closely resembling the results of subsequent analyses (see Figs. 9a, 9b, 10a, 10b), and Brothers's (1975) tree, for the taxa showing ambiguity (Plumariidae placed as the sister group either of the remaining Chrysidoidea or of (Apoidea + Vespoidea)). It differs from Brothers's tree (Fig. 1) in a number of respects: Sierolomorphidae is basal in Vespoidea, (Pompilidae + Rhopalosomatidae) is polyphyletic, Formicidae is the sister group of Bradynobaenidae, and Thynninae s.l. is basal in Tiphiidae. Brothers's major conclusions on the polyphyly of 'Scolioidae', the sister-group relationship of Scoliidae and Vespidae, and

also of Sapygidae and Mutillidae (including Myrmosinae), and the composition of Bradynobaenidae are confirmed. The 1975 tree is, however, only about 2% longer than the most parsimonious cladogram (408 versus 401 steps, both lengths based on the distribution of states in Table III), and the differences found may thus be of little significance. There is no point in analysing them in greater detail since new data are now available. (Note, however, that the computer-derived optimization of states shown in Fig. 1 and Appendix IB differs in many respects from the placement of states used in 1975 (Appendix IA). In particular, the computer-derived scheme suggests that the polarities of at least four characters (25, 61, 62 and 82 = Variables 40, 103, 106 and 142) may be incorrect, since derived states of those characters are placed on the basal stem of the cladogram, and it entails 73 reversals (83 under accelerated transformation only and 48 under delayed transformation only) as compared with only 20 reversals in the 1975 scheme. The distribution of character states on Fig. 8b (Appendix V) suggests that Character 82 may be correctly polarized, however. In deriving his tree, Brothers (1975) used parsimony but rejected its strict application if contra-indicated on the basis of reasonable evolutionary expectations, including the reversal of complex characters.)

In order to take subsequent work and the discovery of new taxa into account, we extended the data matrix based on Brothers's (1975) paper to include those new characters and taxa used by Brothers (1976), Rasnitsyn (1980, 1988), Carpenter (1986), Johnson (1988) and Kimsey (1991) which we were able to code with reasonable certainty and considered to be valid (e.g., see above account of Kimsey's paper). We reinterpreted some characters where indicated by workers such as Gibson (1985) and our new insights, added a few characters, and corrected a few errors discovered in previous analyses. Sclerogibbidae, Embolemyidae, Dryinidae, Bethyloidea, Chrysidoidea, Heterogynaeidae, Diamminae and Proscoliinae were entirely newly scored. *Olixon* was separately scored in order to check whether its placement in Rhopalosomatidae is correct, and Fedtschenkiinae was separately scored to check its association with Sapyginae. Scolioidea (now more properly Scoliinae) and

Rhopalosomatidae (now only the macropterous species, including *Liosphex* Townes) were also rescored to reflect the addition of Proscoliinae and separation of *Olixon* respectively; Thynninae and Sapyginae were rescored to reflect their separation from Diamminae and Fedtschenkiinae respectively; and Scoliidae was rescored to reflect consideration of *Ycaploca* Nagy (Appendix VI, Table IV). Ground-plan character states for taxa newly scored or rescored and new characters were based on the examination of representative specimens (most unfortunately unidentified), supplemented by reference to the papers cited above and to others such as Olmi (1984), Evans (1987) and Kimsey & Bohart (1990).

The 64 most parsimonious cladograms which resulted from analysis of the 219 variables and 34 final taxa all confirm Apoidea as including Heterogynaeidae, (Proscoliinae + Scoliinae) as holophyletic and (*Olixon* + rhopalosomatids) as holophyletic, as shown by the strict consensus tree (Fig. 9a). This also indicates five distinct lineages within the Vespoidea, the relationships between which are unresolved: Sierolomorphidae, Pompilidae, (Sapygidae + Mutillidae), Tiphidae and (Rhopalosomatidae + ((Vespidae + Scoliidae) + (Formicidae + Bradynobaenidae))). The relationships between Fedtschenkiinae, Sapyginae and Mutillidae (including Myrmosinae) are also unresolved. Successive approximations character weighting resulted in two cladograms, one of which is identical to one of the original eight. That one (Fig. 9b) is additionally preferred on the basis of manual optimization of states on the consensus tree (see above; Variables 7 and 214), and also because it is the one most closely resembling the results of subsequent analyses (see Figs. 10a, 10b) for the taxa showing ambiguity (Thynninae s.s. placed as the sister group either of Diamminae or of (Tiphidae to Methochinae)). It resolves the relationships of the major lineages of Vespoidea and agrees substantially with Brothers's (1975) tree (Fig. 1). It differs mainly in the basal position of Sierolomorphidae in Vespoidea, the association of Pompilidae with (Sapygidae + Mutillidae) and its separation from Rhopalosomatidae, and the sister-group relationship of Formicidae to Bradynobaenidae. The relationships of subfamilies within

families (including those of Tiphidae, making allowance for the inclusion of Diamminae in Thynninae s.l. by Brothers) also agree with Brothers's tree, except that Myzininae is basal to Methochinae (but a tree differing only in showing Myzininae and Methochinae as sister-groups, as found by Brothers, has the same raw length, and such a relationship is shown in half of the original trees). Note that the placement of Thynninae s.s. differs from that suggested by Kimsey (1991) who showed it as the sister group of Myzininae; this is due to different treatment of some characters (see our above discussion of Kimsey's paper). Sapyginae and Fedtschenkiinae are now shown as holophyletic. The unexpected basal position of apids in the Apoidea probably reflects the inadequacy of these data for analysing the components of that superfamily. The relationships of the families of Chrysidoidea are identical to those found by Carpenter (1986) (Fig. 5), despite the fact that those taxa are now included within a much larger analysis, giving confidence in the correctness of this result. The distribution of the character states on Fig. 9b is given in Appendix VII.

In order to eliminate any influences on the parsimony analysis of homoplastic occurrences of states in taxa outside the Vespoidea, that taxon was then analyzed in isolation from the Chrysidoidea and Apoidea. Thirty most-parsimonious cladograms resulted (length 471, consistency index 0.51, retention index 0.62) and the strict consensus tree has a topology identical to that of the applicable portion of Fig. 9a except that Diamminae, Thynninae and the higher tiphiids form a trichotomy. Successive approximations character weighting produced one cladogram, identical to one of the original eight, and with a topology identical to the applicable portion of Fig. 9b, except that Myzininae and Methochinae are sister-groups, agreeing with Brothers (1975) and Kimsey (1991) when disregarding her placement of Thynninae, as discussed above. A sister-group relationship of Methochinae with (Tiphinae + Brachycistidinae) is supported by one uniquely derived variable (137, form of mesosoma when apterous) which is not shown in the same state in Brachycistidinae and is not even expressed in Tiphinae, whereas the sister-group relationship of Myzininae and Methochinae is supported by one

uniquely derived and unreversed variable (1, sexual dimorphism in body proportions), which is probably a more significant character. We thus consider this latter arrangement of the subfamilies of Tiphidae as preferable.

Examination of Fig. 9b and Appendix VII suggests that Variables 43 (prosternum, weight 0), 80 (metathoracic-propodeal pleural suture ventral to endophragmal pit, weight 2), 84 (extent of forewing venation, weight 1), 102 (hindwing empusal, anal and jugal veins, weight 2), 118 and 121 (meso- and metatibial spines, weight 2), 164 (male seventh metasomal sternum, weight 0), 193 (mesocoxal subdivision and insertion, weight 0), 197 (mandibles, weight 2), and 198 (female cerci, weight 10) may be incorrectly polarized since derived states of all of these are placed on the basal stem. Of these, only Variables 80 (but only State 2), 84, 102 and 198 are considered unlikely to show reversals; the rest are mostly highly plastic variables which ended up with relatively low weights (2 or less) and their polarities should probably be re-evaluated. Variable 80 also has low weight and should also probably be re-evaluated; it is placed without any reversal of its 'irreversible' state. Variable 198 is definitely correctly polarized, with State 1 found in all aculeates, contrary to Rasnitsyn's (1988) statement. Variables 84 and 102 are unlikely to be incorrectly polarized. State 1 of Variable 84 entails some reduction in the extent of the forewing venation, and is shown on the tree as having six derivations and two reversals; manual optimization ensuring no reversals would involve only a single extra step, so is perhaps preferable, especially since there may be a correlation between smaller size and reduction in venation in some taxa. Variable 102 involves sequential loss of the jugal, anal and empusal veins of the hindwing; an apparent jugal bar is present only in a few sphecids, and it is conceivable that it is not homologous with the same structure elsewhere, so that the reversal to the 0 state there may be reasonable; an anal vein forming a spur from the empusal vein is perhaps less likely to reappear after loss, but optimization ensuring no reversals of State 2 to State 1 would entail seven derivations instead of one derivation and two reversals and may thus be unlikely, since it is possible that the anal vein may persist fused with the empusal

vein at the base even when it has apparently been lost.

It is further evident that another four of the variables for which reversals are considered unlikely are placed with reversals having occurred (2, 96, 161 and 178). Variable 2 (sexual dimorphism in wing development) provides an interesting case where the first derivation of a state is placed at a point which indicates the potential for expression of the state rather than its actual expression, and reversals are thus more apparent than real; State 1 is derived within the Tiphidae just below the point at which Diamminae branches off, and it is expressed in all taxa distal to that point with apterous females; taxa with macropterous females do not show the derived state and so are indicated as having reversals, but they probably nevertheless have the potential for expression of the derived state as shown by various apterous or brachypterous species, for example within Myzinae. State 1 of Variable 96 entails the loss of cell C in the hindwing through the distal reduction of vein C; manual optimization ensuring no reversals would involve nine derivations, so is difficult to evaluate, but may be preferable to the two derivations and five reversals shown. State 1 of Variable 161 entails the loss of the valvelli on gonapophysis VIII of the female; it is shown with five derivations and a single reversal (in Apterogyninae, the only member of the Bradynobaenidae with valvelli); optimization ensuring no reversals would involve another three derivations, but the likelihood of this being correct is difficult to evaluate in the absence of information on the function of these structures. Variable 178 (larval spiracles) is treated in the same way as by Brothers (1975), with an apparent reversal accepted in Sapygidae.

In order to remove any influences of homoplastic character state changes within families and to ensure that all of the taxa included were at a more or less consistent taxonomic level, family ground plans were derived for the Vespoidea, eliminating all subfamilies and single genera (Table V). For each family, the ground-plan state of each variable was specified as the relatively most plesiomorphic state found in any of its component taxa (unless there were *a priori* indications that some other state is more likely to have been that present in the

ancestor) or as the known state where states are unknown in some component taxa. Analysis of the family ground plans of Vespoidea in isolation from the other taxa (except for an hypothetical ancestor) produced five most parsimonious cladograms (length 248, consistency index 0.65, retention index 0.43) and successive approximations character weighting resulted in three cladograms (weighted length 1088), all of which are amongst the initial five. Successive weighting was thus not very informative, and the strict consensus tree of the original five cladograms showed Tiphidae as basal, with the remaining families forming a holophyletic group. The relationships of five lineages were unresolved: Sierolomorphidae, Pompilidae, Rhopalosomatidae, (Mutillidae + Sapygidae), and (Bradynobaenidae + (Formicidae + (Vespidae + Scoliidae))).

It would have been ideal if we could have treated the entire Aculeata in the same way, and derived similar family ground plans for the taxa of Apoidea, especially since there are strong indications that Sphecidae s.l. is paraphyletic with respect to the bees (Lomholdt 1982, Alexander 1990, 1992), but such data are not yet available. Analysis of the family ground plans of Chrysidoidea and Vespoidea and the three taxa of Apoidea together (20 taxa in total, as coded in Tables IV and V) produced four most parsimonious cladograms (strict consensus tree in Fig. 10a) and successive approximations character weighting produced two cladograms, one of which (Fig. 10b) is amongst the original four and is additionally preferred on the basis of manual optimization of variables (36, 126, 180, 193) on the consensus of the two, and because it has the same arrangement as the strict consensus tree (Fig. 10a) for the taxa showing ambiguity (Heterogynaidae or apids basal in Apoidea). The weighted tree agrees very closely with the comparable branches of its counterpart based on all taxa (Fig. 9b), differing only in the basal placement of Heterogynaidae in Apoidea, and the sister-group relationship of Formicidae to (Vespidae + Scoliidae) rather than to Bradynobaenidae (an arrangement also shown unequivocally in the analysis of vespoid family ground plans in isolation, see above). The relationships within the Apoidea are based on poor representation, but the arrangement shown in Fig. 10b is to be

preferred on a number of grounds: although the strict consensus tree based on all taxa (Fig. 9a) shows the structure of Apoidea unresolved, the strict consensus tree based on family ground plans (Fig. 10a) shows Heterogynidae as always basal; furthermore, Heterogynidae has a relatively basal position in Apoidea according to Alexander (1992), although it falls within the Sphecidae s.l. The sister-group relationship of Formicidae to (Vespidae + Scoliidae) is also to be preferred on various grounds: such a relationship is supported by three unique and unreversed derivations on Fig. 10b (34:1, truncate posterolateral angle of pronotum, although also derived within Mutillidae and Tiphiidae (Fig. 9b); 38:2, ventrally produced acute ventral angle of pronotum, although apparently reversed within Scoliidae (Fig. 9b); and 106:1, loss of basal hamuli, although also derived within Bradynobaenidae and Tiphiidae (Fig. 9b)), as contrasted with only one such derivation (150:1, petiole metasoma, a rather variable character within many taxa; 55:1, shortened mesepimeron, is also derived in apids and within Rhopalosomatidae (Fig. 9b)) supporting a sister-group relationship between Formicidae and Bradynobaenidae, as found when altering the topology of Fig. 10b appropriately and as shown in Fig. 9b and Appendix VII; furthermore, this relationship agrees with that found in the analysis of Vespoidea family ground plans only, and with that previously found by Brothers (1975). The relationships within the Vespoidea differ from Brothers's (1975) tree (Fig. 1) only in the more basal position of Sierolomorphidae and the sister-group relationship of Pompilidae with (Mutillidae + Sapygidae) rather than Rhopalosomatidae. The relationships of the families of Chrysidoidea are still identical to those found by Carpenter (1986) (Fig. 5). Fig. 10b thus seems to be the best estimate that we now have of the relationships of the families of Chrysidoidea and Vespoidea, and of the relationships of the three superfamilies.

The distribution of the character states on Fig. 10b is given in Appendix VIII. This suggests (as for Fig. 9b, Appendix VII) that Variables 43, 80, 84, 102, 118, 121, 193, 197 and 198 may be incorrectly polarized since derived states of all of these are placed on the basal stem, and two additional 'irreversible' variables (96, closed cells in hindwing

and 178, larval spiracles) have been placed showing reversals. The same comments apply here as were made above (in discussing Fig. 9b).

When the preferred intrafamilial relationships (as derived from Fig. 9b and analysis of all vespoide taxa in isolation, see above) are added to Fig. 10b, the cladogram shown in Fig. 11 results (distribution of character states given in Appendix IX). Despite the fact that it is slightly longer than the most parsimonious cladograms derived from the full analysis (692 vs 689 steps, a difference of 0.4%, resulting solely from the placement of Formicidae as the sister-group of (Vespidae + Scoliidae) which is strongly justified above), we consider it our current best estimate of the relationships of all of the groups analyzed.

CONCLUSION

Our re-evaluation of Brothers's (1975) and Carpenter's (1986) data and analyses and the incorporation of subsequent contributions and some new data, confirms their results and conclusions in all major respects. Chrysidoidea is definitely a holophyletic group which includes Plumariidae as its most basal taxon, Scoliidae the next most basal, and (Bethyidae + Chrysididae) as the sister-group of (Sclerogibbidae + (Dryinidae + Embolemidae)). Apoidea s.l. and Vespoidea s.l. together form a holophyletic group, as does Vespoidea s.l. itself, although this is less strongly supported. Sierolomorphidae forms a distinct basal clade in Vespoidea. Rhopalosomatidae is probably the sister-group of (Bradynobaenidae + (Formicidae + (Scoliidae + Vespidae))), rather than of Pompilidae, which appears to be the sister-group of (Sapygidae (including Fedtschenkiinae) + Mutillidae (including Myrmosinae)). Tiphiidae is most likely the sister-group of (Pompilidae + (Sapygidae + Mutillidae)). Sierolomorphidae is thus probably more basal in Vespoidea than Brothers (1975) thought, and his suggested relationship of Pompilidae to Rhopalosomatidae was also probably incorrect.

It must be appreciated, however, that most of the characters and states used are essentially those of Brothers (1975) and Carpenter (1986). Although we have used various characters introduced by

Rasnitsyn (1980, 1988), we have often been unable to check their validity and generality of distribution over all of the taxa coded, but have had to rely on his interpretations and statements; these are difficult to evaluate because he did not list the species he had examined and often did not explain the characters fully. It is thus likely that our interpretations and/or codings are incorrect in at least some cases. For example, some Pompilidae have indications of posteromesal expansion of the metapostnotum, which might perhaps be interpreted as a stage intermediate between that in other Pompilidae and the Apoidea; does this mean that pompilids are closer to apoids, or is it an independent trend? Such questions can only be answered if other workers undertake more complete evaluations of particular taxa, looking at a greater variety of representatives than we were able to do, checking the validity of the characters and states used here, and finding new characters. We hope that this paper will stimulate such studies. Meanwhile, it is interesting that the full analysis produced results quite similar to the uncorrected Hennig86 analysis of Brothers's characters only (Fig. 8) and analysis of his taxa using only his characters but modified and corrected as above produced an arrangement essentially identical to that found using all characters, which indicates that the results will probably prove to be fairly stable to further investigations. We are thus satisfied that the present analysis, as presented in Fig. 11, represents the most complete and most rigorous estimate of relationships between the higher taxa of Aculeata (particularly the Chrysidoidea and Vespoidea) now possible.

Bearing in mind the limitations of the data base, uniquely derived and unreversed synapomorphies (sometimes with subsequent derivations) characterizing the superfamilies, families and other major lineages are as follows:

Chrysidoidea: all femora of female inflated (Variable 111: State 1), first metasomal tergum anteriorly narrowed and fused with sternum (152:1), gonocoxite IX of female with articulation within it (160:1), third phragma narrowed and muscles *2ph-3ph* with widely separated posterior attachments (186:1), prothoracic furca proclined (207:1), forewing vein Cu2 reduced (215:1).

Chrysidoids except for Plumariidae: forewing with seven (or fewer) cells (85:2), hindwing with one closed cell (98:1) which has been lost in all extant members, third phragma lost medially (186:2), second phragma scarcely oblique with anterior attachment of muscles *2ph-3ph* (191:1), and anterior pedicels of tentorium rodlike (206:1).

Plumariidae: mesosoma of apterous female uniquely modified (143:1), and seventh metasomal tergum of female concealed under sixth tergum but not desclerotized (159:1); in addition propleura forming short anterior necklike region (41:1, separately derived in Sclerogibbidae).

Remaining chrysidoids: posterior margin of metapostnotum mesally indistinct (64:1), inner metatibial spur calcariform with dorsal blunt longitudinal setose carina (136:1), and third phragma absent (186:3).

Scolebythidae: propleura widely separated posteriorly (42:1), protrochanter inserted near base of coxa (45:1), hindwing with vein C long and vein SC+R+S absent (98:2), meso- and metatibiae with long slender setae only (120:1, 123:1).

Bethylidae and Chrysididae: metapostnotum mesally shortened and hidden (64:2), vein C short but distinct and vein SC+R+S long (101:1), and gonocoxite IX and gonapophysis 1 IX in female not articulated (203:1).

Bethylidae: hindwing with vein C absent except at extreme base and vein SC+R+S very short (101:2), head prognathous of 'bethylid type' (209:1), and clypeus with median longitudinal carina (211:1).

Chrysididae: metasoma with only four exposed terga (157:1), and larval host Tenthredinoidea cocoon or Phasmida egg (204:3).

Sclerogibbidae, Dryinidae and Embolemidae: hindwing with empusal vein minute, anal and jugal veins absent (102:3), furcula in ovipositor absent (202:1).

Sclerogibbidae: frontal ledge overhanging ventrally-facing antennal socket (8:1), compound eye with dense pores and short setae (13:2), more than 14 antennomeres (19:1), prepectus fused midventrally but not to mesepisternum (53:1), forewing with six closed cells (87:1), hindwing with vein C short and vein SC+R+S

- absent (100:1), profemur of female much swollen and protibia expanded (111:2), foreleg with arolium much enlarged (114:1), mesosoma of apterous female uniquely modified (144:1), seventh metasomal tergum of female hidden under expanded sixth sternum (158:1), larval host Embioptera (204:1), and prothoracic furca proclined and modified (207:2).
- Dryinidae and Embolemidae: ten antennomeres (20:1), hindwing with veins C and SC+R+S long but fused (99:1), larval host Auchenorrhyncha (204:2), and larva initially endoparasitic but then forming external cyst (205:1).
- Dryinidae: forewing with five closed cells (86:2).
- Embolemidae: prepectus large and fused midventrally and to pronotum (32:2, 53:2), metapleuron uniquely modified (66:2), mesosoma of apterous female uniquely modified (144:2), anterior pedicels of tentorium rod-like with lamellar processes (206:2), antennal prominence present (212:1), pedicel-flagellum articulation fixed (213:1).
- Aculeata *sensu stricto*: male with 13 and female with 12 antennomeres (18:1), and seventh metasomal tergum of female hidden and substantially desclerotized (156:1).
- Apoidea (subordinate taxa not further analyzed because of inadequate data): pronotum with posterolateral angle reduced above spiracular lobe (35:1), ventral angle of pronotum considerably produced mesad (39:1), prepectus fused midventrally and to mesepisternum (52:1), metapostnotum expanded posteromesally to form 'propodeal triangle' (65:1), and second phragma scarcely oblique with posterior attachment of muscles *2ph-3ph* (192:1).
- Vespoidea: no unique and unreversed derivations, but prepectus reduced (48:1, also in Chrysidae), and hypopharyngeal pubescence reduced (194:1, but reversed in Rhopalosomatidae and Pompilidae).
- Sierolomorphidae: forewing with seven closed cells (88:1), hypopygium of male peglike (165:1), and third phragma weakly expanded laterally with muscles *2ph-3ph* small and attaching on somewhat separated areas of phragma (190:1).
- Vespoidea except Sierolomorphidae: hindwing with jugal lobe moderately reduced (108:1); in addition, metapostnotum partially invaginated and mesally reduced (63:1, but reversed in Rhopalosomatidae and Pompilidae).
- Rhopalosomatidae to Scolidae: no unique and unreversed derivations, but prepectus further narrowed and shortened (48:2, separately derived in Brachycistidinae) and junction of first and second metasomal terga slightly constricted (149:1, but reversed in Vespidae and separately derived in Tiphiinae and Brachycistidinae).
- Rhopalosomatidae: forewing with cell C almost eliminated (92:1), female with tarsi flattened and forelegs swollen (112:1), larval host Gryllidae only (204:7), and larva entirely ectoparasitic with cyst formation (205:2).
- Bradynobaenidae to Scolidae: no unique and unreversed derivations, but mesad mesocoxal articulations posteriorly displaced (57:1, separately derived in Mutillidae).
- Bradynobaenidae: mesocoxae somewhat separated and metasternum laterally depressed and slightly anteriorly produced (75:1, 78:1), mesosoma of apterous female uniquely modified (141:1), lateral felt line on second metasomal tergum only (146:1), first metasomal tergum overlapping sternum only posteriorly (151:1), and possibly larval host Solifugae (204:9) (uniquely derived paired stridultra on fourth metasomal tergum (148:1) lost in two subfamilies).
- Formicidae to Scolidae: no unique and unreversed derivations, but ventral angle of pronotum acute and produced (38:2, but reversed in Proscoliinae).
- Formicidae: caste of sterile females present (3:1), metapleural gland present (72:1), inner meso- and metatibial spurs calcariform with dorsal pectinate carina (128:1, 134:1), mesosoma of apterous female uniquely modified (144:3), larval food relocated and nest constructed but not closed (181:1).
- Vespidae and Scolidae: posterolateral angle of pronotum dorsally produced above anterior margin of tegula (34:2), and third phragma expanded laterally with muscles *2ph-3ph* very large (190:3); in addition, prey relocated, nest constructed and closed (180:2, separately derived in apids which use dissimilar provisions),

- and head of larva with strong parietal bands (217:1, separately derived in Pompilidae).
- Vespidae: pronotum fused with much-reduced hidden prepectus and closely abutting mesepisternum (32:1, 48:3), and posterolateral margin of pronotum acutely produced and much exceeding anterior margin of tegula (34:3).
- Scoliidae: pronotum immovable with prepectus fused with mesepisternum (31:1), mesocoxae widely separated without shortening of mesosternum (59:1), metasternum broad and not depressed (76:1), metacoxae widely separated (79:1), protibial calcar inwardly curved and posteriorly hollowed (117:1), spines on meso- and metatibiae very strong and scattered (119:1, 122:1), hypopygium of male elongate and apically trilobed (166:1), and gonapophyses IX (penis valves) of male with dorsal membranous link over most of length (172:1).
- Tiphiidae to Sapygidae: no unique and unreversed derivations, but second thoracic spiracle of larva reduced (178:1, reversed in Sapyginae).
- Tiphiidae: hindwing with distal origin of crossvein cu-c (103:1); in addition, mesosternum with platelike projections posteromesally (56:2, lost in Methochinae, but also present in Rhopalosomatidae).
- Pompilidae to Sapygidae: prepectus not shortened and fused with mesepisternum (51:1).
- Pompilidae: larval prey relocated into pre-existing cavity which is then closed (182:1), and larval prey Araneae (204:6); in addition, inner metatibial spur calcariform with basal tuft of bristles and dorsal pectinate carina (132:1, separately derived in Rhopalosomatidae), and larval head with strong parietal bands (217:1, separately derived in Vespidae and Scoliidae).
- Mutillidae and Sapygidae: hindwing with jugal lobe small (108:2), gonapophyses IX (penis valves) of male linked only basally by membrane (173:1), and larval host Aculeata larva or pupa (204:5).
- Mutillidae: prepectus uniquely modified and fused with mesepisternum (51:2), mesosoma of apterous female uniquely modified (139:1), and third metasomal tergum with single small stridulitrum (147:1).

Sapygidae: no unique and unreversed derivations but, prementum and stipes elongated (23:1, separately derived in apids).

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APPENDIX I

Distribution of derived character states for Aculeata on cladogram derived by Brothers (1975:Fig. 2). Internodes are referred to by numbers which designate the inferred ancestors subtending each internode in the original figure and taxon names referring to the range of taxa subtended. Character state code numbers are those used in the original text. Square brackets indicate an intermediate state not present but probably necessary for derivation of a more derived state; reversals are indicated by (r).

A. Distribution of states as derived by Brothers (1975) (NOT those plotted in Fig. 1). States occur in both sexes (or are consistently sexually dimorphic) unless otherwise indicated (for states which could occur in either sex—; F=female, M=male).

- 1-2** (Chrysidoidea): 42.1; 45.1; 46.1; 51.2; 56.2; 79.1
Plumariidae: 2.1; 7.3F; 9.3F; 10.1F; 13.1F; 16.1F; 17.1F; 18.1M; 20.1F; 24.2F; 25.1; 27.1M; 38.1; 38.1.1M; 57.1F; 59.1F; 61.1; 61.1.1F; 62.1; 69.4; 80.1; 82.1
- 2-3**: 35.2; 46.1.1; 49.1; 50.3
Scolecithyidae: 5.1; 7.3; 9.1; 20.1; 26.2; 34.2; 46.1.1.1; 49.1.1; 50.3.1; 57.2; 61.2; 62.2
- bethylids** ('higher' Chrysidoidea): 17.1
- 1-4**: 12.1; 25.1; 26.1; 61.1; 62.1; 78.1
- 4-5** (Apoidea): 18.2; 21.2; 22.1; 23.2; 27.1; 29.2; 31.2; 33.1; 35.3; 36.3; 39.1; 47.1; [64.1] 64.1.1; 81.2; 90.1
- apids** (Apidae s.l.): 4.1; 15.1; 30.2; 42.1; 45.1; 50.1; 51.1; 63.1; 78.1.1; [82.1] 82.1.1; 84.2; 85.1; 87.2; 89.1; 90.1.1; 92.1
- sphecids** (Sphecidae s.l.): 21.2.1; 61.1.1; 62.1.1
- 4-6** (Vespoidea): 24.1; 29.1; 38.1; 51.2; 56.1
- 6-7**: 31.1; 35.1; 52.1; 61.1.1; 62.1.1; 64.1F; 82.1; 88.1
- 7-8**: 6.1; 29.1.2; 38.1.1; 50.1; 53.1; 55.1; 56.1.1; 64.1.1F; 66.1; 86.2; 90.2
- Sapygidae**: 15.3; 80.1; 87.2; 88(r)
- 8-9** (Mutillidae): 2.1; 13.1; 14.1; 29.1.2.1; 32.1; 36.1; [42.1] 42.1.1; 54.1; 69.2; 71.1; 72.1; 76.1; 81.1
- Myrmosinae**: 9.2; 58.1F; 59.1F; 66.1.1; 69.2.1; 82(r); 84.2
- mutillids** ('higher' Mutillidae): 18.1; 21.1; 30.1; 34.1; 38.1.1.1; 45.1; 49.1; 69.2.2; 70.1
- 7-10** (Tiphidae): 31.1.1; 57.1F
- Anthoboscinae**: 45.1F; 84.1
- 10-11**: 69.1
- Thynninae** (s.l.): 2.1; 55.1; 66.1
- 11-12**: 69.1.1; 72.1M; 76.1; 83.3
- 12-13**: 1.1; 6.2; 82(r)
- Myzininae**: 35.1.1
- Methochinae**: 2.1; 7.3; 9.2; 22.1; 31.1(r); 42.1; 46.3; 50.1; 57(r); 61.1(r); 62.1(r); 63.1F; 65.2; 66.1M; 67.1; 68.4; 81.1; 90.2
- 12-14**: 21.1; 22.1; 33.1; [36.1] 36.1.1; 42.1; 44.1; 45.1; 49.1; 66.1; 72.1; 81.1; 82.1.1; 84.2; 85.1
- Tiphiinae**: 35.1.1; 42.1.1; 46.4
- Brachycistidinae**: 2.1; 5.1F; 7.3F; 8.1; 9.1M; 9.3F; 10.1F; 18.1M; 27.1M; 29.1.1; 54.2; 59.1; 63.1; 69.1.1.1
- 6-15**: 22.1; 38.1.1; 55.1
- Sierolomorphidae**: 9.1; 31.1; 36.2; 42.1; 45.1; 46.2; 49.1; 50.1; 56.2; 66.1; 83.1; 84.2
- 15-16**: 47.1; 54.1; 87.1
- 16-17**: 31.1; 32.1; 36.2; 48.1; 50.1; 68.1; 82.1
- Pompilidae**: 29.1.2; 33.1; 61.1.1; 62.1.1; 64.1; 80.1; 88.1; [90.1] 90.1.3
- Rhopalosomatidae**: 9.1; 18.1; 21.1; 27.1; 29.1.1; 31.1.1; 45.1; 46.1; 49.1; 55(r); 57.3F; 72.1; 81.2; [87(r)] 87.3
- 16-18**: 29.1.1; 33.1; [35.1] 35.1.1; 76.1
- 18-19**: 18.1; 21.1; 23.1; 27.1; 36.1; 54.2; 90.1
- Formicidae**: 3.1; 9.1; 29.1.3; 30.2; 33.1.1; 37.1; 46.1; 50.1; [61.1.1] 61.1.1.1; [62.1.1] 62.1.1.1; 65.1; 68.3; 72.1; 73.1; 81.2; 89.1; 90.1.2; 91.1
- 19-20**: 5.2; 7.2; 15.2; 19.1; 21.1.1; 25.1.1; 31.2; 48.1; 85.1
- Scoliidae**: 9.3; 29.1.1.2; 30.1; 32.2; 36.1.2; 38.1.1.2; 39.1; 41.1; 44.1; 45.1; 49.1; 55.1.1; 57.1F; 59.1; 60.2; 61.1.2; 62.1.2; 63.1; 64.1; 72.1; 83.2; 84.2; 86.1
- Vespidae** (s.l.): 21.1.1.1; 29.1.1.1; 32.1; 43.1; 68.2; 80.1; 82.1; 89.1; 90.1.1; 91.1
- 18-21** (Bradynobaenidae): 2.1; 9.1; 10.1F; 30.2; [38.1(r)] 38(r); 39.1; 40.1; 42.1; 45.1; 49.1; 55.1.1; 69.3; 70.2; 71.2; 72.1; 73.1; 74.1; 81.2; 82.1
- 21-22** (Typhoctinae): 4.1; 22(r); 36.2; 66.1; 69.3.1; 80.1
- Eotillini**: 47(r); 50.1; 55.1(r); 55(r); 58.1
- Typhoctini**: [56(r)] 56.2; 61.1.1; 62.1.1
- 21-23**: 6.1; 7.1; [9(r)F] 9.3F; 13.1; 18.1M; 23.1; 27.1M; 36.1; 57.1F; 58.1F; 61.1.1; [62.1.1] 62.1.1.1; 64.1F; 69.3.2; 74.1.1; 75.1; 83.4
- Chyphotinae**: 7.1.1F; 8.1; 33.1.1; 47(r); 50.1; 66.1M; 75.1.1F; 80.1; 84.1
- 23-24**: [9(r)] 9.3; 11.1; 28.1; 32.2; 34.1; 40.1.1; 45.1.1; 46.5; 47.1.1; 49.1.1; [54(r)] 54.2; 58.1; 60.1; 61.1.1.1; [64.1] 64.1.2; 70.2.1F; 71(r); 85.1
- Apterogyninae**: 5.2M; 7.1.1F; 8.1; 66.1; 72.1.1; 77.1
- Bradynobaeninae**: 6.2; 15.4; 16.2; 17.1; 21.3; 28.1.1; 36.1.1; 43.1; 44.1; 46.5.1; 50.2; 59.1; 60.1.1; 61.1.1.1.1; 62.1.1.1.1; 63.2; 64.1.2.1; 64.1.2.1.1F; 70.2.1; 80.1; [81(r)] 81.1; 83.4.1

B. Distribution of states for data in Table III as applied to tree (Fig. 1) with topology identical to that of Brothers (1975); optimizations by Clados (Nixon 1992) using accelerated transformation (approach of Farris, 1970), except using delayed transformation (approach of Swofford & Maddison 1987) for variables considered unlikely to show reversals. For treatment of sexually dimorphic characters, see text. Placements which agree with those above (1A) are indicated in boldface.

- Aculeata-1**: 25.1; 61.1; 62.1; 82.1
- 1-2** (Chrysidoidea): **42.1; 45.1; 46.1; 51.2; 56.2; 79.1**
- Plumariidae**: **2.1; 10.1; 24.2; 25.1; 38.1; 57.1; 69.4; 80.1**
- 2-3**: 25(r); **35.2; 46.1.1; 49.1; 50.3**; 61(r); 62(r); 82(r)
- Scolecithyidae**: **5.1; 7.3; 9.1; 20.1; 26.2; 34.2; 46.1.1.1; 49.1.1; 50.3.1; 57.2; 61.2; 62.2**
- bethylids** ('higher' Chrysidoidea): **17.1**

1-4: 12.1; 22.1; 26.1; 50.1; 61.1.1; 62.1.1; 78.1
 4-5 (Apioidea): 18.2; 21.2; 23.2; 27.1; 29.2; 31.2; 33.1;
 35.3; 36.3; 39.1; 47.1; 51(r); [64.1;] 64.1.1; 81.2;
 90.1
 apids (Apidae s.l.): 4.1; 15.1; 30.2; 42.1; 51.1; 61.1(r);
 62.1(r); 63.1; 78.1.1; 82.1.1; 84.2; 85.1; 87.2; 89.1;
 90.1.1; 92.1
 sphecids (Sphecidae s.l.): 21.2.1; 50(r); 82(r)
 4-6 (Vespoidea): 24.1; 29.1; 31.1; 38.1; 51.2; 55.1; 66.1
 6-7: 22(r); 35.1; 52.1; 56.1
 7-8: 6.1; 29.1.2; 53.1; 56.1.1; 86.2
 Sapygidae: 15.3; 80.1; 87.2
 8-9 (Mutillidae): 2.1; 13.1; 14.1; 29.1.2.1; 32.1; 36.1;
 [42.1;] 42.1.1; 54.1; 69.2; 71.1; 76.1; 81.1; 88.1;
 90.2
 Myrmosinae: 9.2; 66.1.1; 69.2.1; 82(r); 84.2
 mutillids ('higher' Mutillidae): 18.1; 21.1; 30.1; 34.1;
 [38.1.1;] 38.1.1.1; 45.1; 49.1; 69.2.2; 70.1
 7-10 (Tiphidae): 31.1.1; 38(r); 50(r); 55(r); 57.1; 88.1
 Anthoboscinae: 66(r); 84.1
 10-11: 2.1
 Thynninae (s.l.): 55.1; 69.1
 11-12: 22.1; 76.1; 81.1; 83.3
 12-13: 1.1; 6.2; 66(r); 82(r)
 Myzininae: 2(r); 22(r); 35.1.1; 81(r)
 Methochinae: 7.3; 9.2; 31.1(r); 42.1; 46.3; 50.1; 57(r);
 61.1(r); 62.1(r); 65.2; 67.1; 68.4; [69.1;] 69.1.1;
 90.2
 12-14: 21.1; 33.1; [36.1;] 36.1.1; 42.1; 44.1; 45.1; 49.1;
 72.1; 82.1.1; 84.2; 85.1
 Tiphinae: 2(r); 35.1.1; 42.1.1; 46.4
 Brachycistidinae: 8.1; 10.1; 29.1.1; 54.2; 59.1; 63.1;
 [69.1;] [69.1.1;] 69.1.1.1
 6-15: 9.1; 36.2
 Sierolomorphidae: 42.1; 45.1; 46.2; 49.1; 56.2; 61.1(r);
 62.1(r); 82(r); 83.1; 84.2
 15-16: 29.1.1; 47.1; 56.1; 66(r); 72.1; 81.2; 87.1
 16-17: 32.1; 48.1; 54.1; 68.1
 Pompilidae: 9(r); 29.1(r); 29.1.2; 33.1; 64.1; 72(r);
 80.1; 81(r); 88.1; [90.1;] 90.1.3
 Rhopalosomatidae: 18.1; 21.1; 27.1; 31.1.1; 46.1;
 49.1; 55(r); 57.3; 61.1(r); 62.1(r); 87(r); 87.3
 16-18: 23.1; 30.2; 31(r); 33.1; [35.1;] 35.1.1; 36(r);
 36.1; 73.1; 76.1; 89.1; 90.1
 18-19: 18.1; 21.1; 27.1; 54.2; 91.1
 Formicidae: 3.1; 29.1.1.3; 33.1.1; 37.1; 46.1; 61.1.1.1;
 62.1.1.1; 65.1; 68.3; 82(r); 90.1.2
 19-20: 5.2; 7.2; 9(r); 15.2; 19.1; 21.1.1; 25.1.1; 30(r);
 31.2; 48.1; 50(r); 61.1(r); 62.1(r); 73(r); 81(r); 85.1
 Scolidae: 9.3; 29.1.1.2; 30.1; 32.2; 36.1.2; [38.1.1;]
 38.1.1.2; 39.1; 41.1; 44.1; 45.1; 49.1; 55.1.1; 57.1;
 59.1; 60.2; 61.1.2; 62.1.2; 63.1; 64.1; 82(r); 83.2;
 84.2; 86.1; 89(r); 91(r)

Vespidae (s.l.): 21.1.1.1; 29.1.1.1; 32.1; 43.1; 68.2;
 72(r); 80.1; 90.1.1
 18-21 (Bradynobaenidae): 2.1; 10.1; 38(r); 39.1; 40.1;
 42.1; 45.1; 49.1; 54.1; 69.3; 70.2; 71.2; 74.1; 80.1
 21-22 (Typhoctinae): 4.1; 22(r); 23(r); 36(r); 36.2;
 66.1; 69.3.1
 Eotillini: 47(r); 55(r); 58.1; 61.1(r); 62.1(r)
 Typhoctini: 50(r); 55.1.1; 56(r); 56.2
 21-23: 6.1; 7.1; 8.1; 9(r); 13.1; 55.1.1; 57.1; 62.1.1.1;
 69.3.2; 74.1.1; 75.1; 83.4
 Chyphotinae: 33.1.1; 47(r); 75.1.1; 84.1
 23-24: 9.3; 11.1; 28.1; 34.1; 40.1.1; 45.1.1; 46.5;
 47.1.1; 49.1.1; 50(r); 54(r); 54.2; 58.1; 60.1; 61.1.1.1;
 64.1; 64.1.2; 71(r); 85.1
 Apterogyninae: 66.1; 72.1.1; 77.1; 80(r)
 Bradynobaeninae: 6.2; 8(r); 15.4; 16.2; 17.1; 21.3;
 28.1.1; 36.1.1; 43.1; 44.1; 46.5.1; 50.2; 59.1; 60.1.1;
 61.1.1.1.1; 62.1.1.1.1; 63.2; [64.1.2.1;] 64.1.2.1.1;
 70.2.1; 81(r); 81.1; 83.4.1

APPENDIX II

Characters and states for Aculeata derived from Rasnitsyn (1980). Character states are linearly ordered except where noted, with the inferred primitive state listed first.

The scores for the taxa are given in Table I. Some corrections have been made, as noted, where these are matters of fact rather than interpretation. Characters are treated as nonadditive where we regard the ordering of states as unclear. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Rasnitsyn did not provide complete lists of diagnostic characters for his phylogenetic tree; where the state for a given taxon is unclear or unknown, we have usually scored it so as to provide the best support for Rasnitsyn's interpretation. Some scores may thus be erroneous. We have included characters dismissed solely on grounds of homoplasy by Rasnitsyn, again in order to assess most accurately the support for Rasnitsyn's scheme provided by all the evidence he discussed. 'Trends' are not included, only ground-plan states. We regard the polarities of Characters 2 and 15 as incorrect (see Brothers 1975, Carpenter 1986).

1. Valvifer 2: Not articulated = 0. Articulated = 1.
2. Hindwing jugal lobe: Absent = 0. Present = 1. Reduced = 2.

3. Anterior pedicels of tentorium: Thick = 0. Rodlike = 1. With lamellar processes = 2.
4. Prothoracic furca: Vertical = 0. Proclined = 1. 'Modified' in Sclerogibbidae = 2.
5. Reduction of forewing venation: 2m-cu present = 0. 2m-cu lost or present only as trace = 1.
6. Valves 2: Articulated with valvifer 2 proximally = 0. Not jointed with valvifer 2 proximally = 1. Secondary processes = 2.
7. Antenna: With 13 articles in both sexes = 0. With 13 articles in male and 12 in female = 1. With 10 articles = 2. With more than 14 articles = 3. NONADDITIVE.
8. Antennal pedicel: Mobile = 0. Fixed = 1.
9. Hosts: Beetles = 0. Embiidina = 1. Auchemorrhyncha = 2. Tenthredinoidea or Phasmida = 3. Melliferous = 4. Aculeata = 5. Araneae = 6. Gryllidae = 7. Wide host range (social foragers) = 8. Solifugae = 9. NONADDITIVE. [The host for Bradynobaenidae is based on new unpublished records.]
10. Host habitat: 'Confined' = 0. Free-living = 1.
11. Life style: Ectoparasitic = 0. Endoparasitic initially, with cyst formation = 1. [Rasnitsyn's original interpretation of complete endoparasitism in emboleimids was an error; see Carpenter (1986), Wharton (1989).]
12. Furcula: Present = 0. Absent = 1. Vertical lamella = 2. NONADDITIVE.
13. Metasomal sternumI: Thin and overlapping sternumII = 0. Thick and abutting = 1. Forming lobules = 2. NONADDITIVE.
14. Metasomal sternum II: Curved anteriorly = 0. Straight with lateral notches = 1. Lateral desclerotized areas expanded = 2. Median notch = 3. NONADDITIVE.
15. Metasternum: Anteriorly narrow = 0. Carinate = 1. Two carinae = 2. Broad = 3. NONADDITIVE.
16. Female metasomal sternumVII: External = 0. Internated = 1.
17. Bilamellar stemming plates of ovipositor: Absent = 0. Present = 1.
18. Hypopharynx pubescence: Present = 0. Reduced = 1.
19. Pronotal lobes: Small = 0. Enlarged = 1.
20. Metapostnotum: Present and unmodified = 0. With propodeal suture obliterated = 1. Forming 'propodeal triangle' = 2. Medially shortened = 3. Medially invaginated = 4. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 35).]
21. Metatibial calcar: Absent = 0. Basal brushes and chitinous modification = 1. Brushed lacking = 2. Brushes only = 3. Dorsally pectinate = 4. Dorsal carinate expansion = 5. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 68).]
22. Arolium and orbicula: Large = 0. Reduced = 1.
23. Metasomal sternumI and tergumII: Not articulated = 0. Articulated = 1.
24. Metasomal tergumI laterotergites: Wide = 0. Reduced = 1.
25. Propleura: Separated = 0. In contact along entire length = 1.
26. Prepectus (first variable): Not extended along pleurosternum = 0. Extended = 1. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 29).]
27. Prepectus (second variable): Broad = 0. Narrowed = 1. Shortened = 2.
28. Prepecti (third variable): Not fused = 0. Long and fused = 1. Line of fusion obliterated = 2.
29. Hindwing anal veins: Present = 0. Reduced = 1.
30. Hindwing axillary excision: Shallow = 0. Deepened = 1.
31. Basal hamuli: Scattered = 0. Closely spaced = 1.
32. Pterostigma: Large = 0. Small = 1.
33. Larval mandibles: Quadridentate = 0. Tridentate = 1.
34. Metaphragma: Narrow = 0. Expanded = 1.
35. Posterolateral angle of pronotum: Not produced = 0. Slightly produced = 1. Exceeding tegula = 2. Forming acute lobe = 3. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 21.).]
36. Mesotibial spines: Absent = 0. Strong scattered spines present = 1. Spines apical = 2. Very strong spines = 3. NONADDITIVE. [We

have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 61).]

37. Mesothoracic lamellae: Absent = 0. Small = 1. Large lobes = 2.
38. Dorsal aedeagal fusion: Sclerotized = 0. Desclerotized = 1.

APPENDIX III

Characters and states for Aculeata derived from Rasnitsyn (1988). Character states are linearly ordered except where noted, with the inferred primitive state listed first.

The scores for the taxa are given in Table II. Characters are treated as nonadditive where we regard the ordering of states as unclear. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix. Rasnitsyn (1988) provided a diagnosis of his phylogenetic scheme, along with notes discussing some characters. This did not include all of the characters dismissed as homoplastic in Rasnitsyn (1980). These characters are included here as coded in Appendix II. Most of the characters mentioned are treated substantially as in Rasnitsyn (1980); the coding for these characters is as in Appendix II. One character from Appendix II is deleted (24, not included by Rasnitsyn, 1988), one is modified to include another state (23, specified more precisely by Rasnitsyn, 1988), and the scores are modified for four characters (17, 23, 36 and 37 in Appendix II). Eight new characters are included; generally, these are characters alluded to by Rasnitsyn (1980) but specified more precisely in 1988. We regard the polarity of Characters 2 and 15 as incorrect; see Brothers (1975), Carpenter (1986). We consider Character 45 as probably invalid; the sulcus referred to is the fused anteromedian lines (see Daly 1964, Matsuda 1970) seen in relatively more apomorphic members of the Apoidea s.l. (Alexander 1992); separate lines are present in most Aculeata (including the relatively more plesiomorphic Apoidea) and Parasitica.

1. Valvifer 2: Not articulated = 0. Articulated = 1.
2. Hindwing jugal lobe: Absent = 0. Present = 1. Reduced = 2.

3. Anterior pedicels of tentorium: Thick = 0. Rodlike = 1. With lamellar processes = 2.
4. Prothoracic furca: Vertical = 0. Proclined = 1. 'Modified' in Sclerogibbidae = 2.
5. Reduction of forewing venation: 2m-cu present = 0. 2m-cu lost or present only as trace = 1.
6. Valves 2: Articulated with valvifer 2 proximally = 0. Not jointed with valvifer 2 proximally = 1. Secondary processes = 2.
7. Antenna: With 13 articles in both sexes = 0. With 13 articles in male and 12 in female = 1. With 10 articles = 2. With more than 14 articles = 3. NONADDITIVE.
8. Antennal pedicel: Mobile = 0. Fixed = 1.
9. Hosts: Beetles = 0. Embiidina = 1. Auchenorrhyncha = 2. Tenthredinoidea or Phasmida = 3. Melliferous = 4. Aculeata = 5. Araneae = 6. Gryllidae = 7. Wide host range (social foragers) = 8. Solifugae = 9. NONADDITIVE. [The host for Bradynobaenidae is based on new unpublished records.]
10. Host habitat: 'Confined' = 0. Free-living = 1.
11. Life style: Ectoparasitic = 0. Endoparasitic initially, with cyst formation = 1. [Rasnitsyn's original interpretation of complete endoparasitism in emboleimids was an error; cf. Carpenter (1986), Wharton (1989).]
12. Furcula: Present = 0. Absent = 1. Vertical lamella = 2. NONADDITIVE.
13. Metasomal sternumI: Thin and overlapping sternumII = 0. Thick and abutting = 1. Forming lobules = 2. NONADDITIVE.
14. Metasomal sternumII: Curved anteriorly = 0. Straight with lateral notches = 1. Lateral desclerotized areas expanded = 2. Median notch = 3. NONADDITIVE.
15. Metasternum: Anteriorly narrow = 0. Carinate = 1. Two carinae = 2. Broad = 3. NONADDITIVE.
16. Female metasomal sternumVII: External = 0. Internated = 1.
17. Bilamellar stemming plates of ovipositor: Absent = 0. Present = 1.
18. Hypopharynx pubescence: Present = 0. Reduced = 1.
19. Pronotal lobes: Small = 0. Enlarged = 1.

20. Metapostnotum: Present and unmodified = 0. With propodeal suture obliterated = 1. Forming 'propodeal triangle' = 2. Medially shortened = 3. Medially invaginated = 4. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 35).]
21. Metatibial calcar: Absent = 0. Basal brushes and chitinous modification = 1. Brushes lacking = 2. Brushes only = 3. Dorsally pectinate = 4. Dorsal carinate expansion = 5. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 68).]
22. Arolium and orbicula: Large = 0. Reduced = 1.
23. Metasomal sternumI and tergumII: Not articulated = 0. Articulated, with rotary mobility = 1. Hinged, no rotary mobility = 2. NONADDITIVE.
24. Propleura: Separated = 0. In contact along entire length = 1.
25. Prepectus (first variable): Not extended along pleurosternum = 0. Extended = 1. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 29).]
26. Prepectus (second variable): Broad = 0. Narrowed = 1. Shortened = 2.
27. Prepectus (third variable): Not fused = 0. Long and fused = 1. Line of fusion obliterated = 2.
28. Hindwing anal veins: Present = 0. Reduced = 1.
29. Hindwing axillary excision: Shallow = 0. Deepened = 1.
30. Basal hamuli: Scattered = 0. Closely spaced = 1.
31. Pterostigma: Large = 0. Small = 1.
32. Larval mandibles: Quadridentate = 0. Tridentate = 1.
33. Metaphragma: Narrow = 0. Expanded = 1.
34. Posterolateral angle of pronotum: Not produced = 0. Slightly produced = 1. Exceeding tegula = 2. Forming acute lobe = 3. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 21).]
35. Mesotibial spines: Absent = 0. Strong scattered spines present = 1. Spines apical = 2. Very strong spines = 3. NONADDITIVE. [We have supplemented Rasnitsyn's account with reference to Brothers (1975: Character 61).]
36. Mesothoracic lamellae: Absent = 0. Small = 1. Large lobes = 2.
37. Dorsal aedeagal fusion: Sclerotized = 0. Desclerotized = 1.
38. Trochantellus: Present = 0. Absent = 1.
39. Prepecti (fourth variable): Separated = 0. In contact = 1.
40. Prosternum: Visible externally = 0. Reduced externally = 1. Almost lost externally = 2. Lost = 3.
41. Mesothoracic venter: Not produced caudally = 0. Produced caudally = 1.
42. Mandibles: 'Chewing type' = 0. 'Cutting type' = 1.
43. Female cerci: Present = 0. Absent = 1.
44. Mesocoxal base: Broad = 0. Narrow, tubular = 1.
45. Median scutal sulcus: Present = 0. Absent = 1.
46. Oviposition sequence: Prey first, then nest construction = 0. Nest construction first, then prey = 1.
47. Female metasomal sternumVI: Convex = 0. Depressed = 1. [38-47 = characters added from Rasnitsyn (1988).]

APPENDIX IV

Variables used in analysis of Aculeata based entirely on Brothers (1975), showing equivalence with character states described there (using nonredundant linear coding); derived states not used because of sexually dimorphic occurrence (see text) enclosed within square brackets.

The scores for the taxa are given in Table III. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Variables considered unlikely to show reversals: 15, 16, 25-27, 30, 48, 49, 56, 69, 72, 75-80, 83-88, 90-92, 94, 95, 99, 105, 108, 109, 110, 116, 121-126, 133, 134, 137, 149, 152-155, 157-161.

1. Sexual dimorphism, general form: Brothers (1975) State I = 0. State I.1 = 1.

2. Sexual dimorphism, aptery: State 2 = 0. State 2.1 = 1.
3. Sterile caste: State 3 = 0. State 3.1 = 1.
4. Pubescence: State 4 = 0. State 4.1 = 1.
5. Clypeus (first variable): State 5 (and 5.2) = 0. State 5.1 = 1.
6. Clypeus (second variable): State 5 (and 5.1) = 0. State 5.2 = 1.
7. Antennal socket (first variable): State 6 (and 6.2) = 0. State 6.1 = 1.
8. Antennal socket (second variable): State 6 (and 6.1) = 0. State 6.2 = 1.
9. Eye form (first variable): State 7 (and 7.2, 7.3) = 0. State 7.1 = 1. [State 7.1.1 = 2; Chyphotinae and Apterogyninae females and within other taxa.]
10. Eye form (second variable): State 7 (and 7.1, 7.1.1, 7.3) = 0. State 7.2 = 1.
11. Eye form (third variable): State 7 (and 7.1, 7.1.1, 7.2) = 0. State 7.3 = 1.
12. Eye contour: State 8 = 0. State 8.1 = 1.
13. Eye pores and setae (first variable): State 9 (and 9.2, 9.3) = 0. State 9.1 = 1.
14. Eye pores and setae (second variable): State 9 (and 9.1, 9.3) = 0. State 9.2 = 1.
15. Eye pores and setae (third variable): State 9 (and 9.1, 9.2) = 0. State 9.3 = 1.
16. Ocelli: State 10 = 0. State 10.1 = 1.
17. Genal organ: State 11 = 0. State 11.1 = 1.
18. Antennal dimorphism: State 12 = 0. State 12.1 = 1.
19. Radicle axis: State 13 = 0. State 13.1 = 1.
20. Radicle-scape insertion: State 14.1 = 0. State 14.1 = 1.
21. Labio-maxillary complex (first variable): State 15 (and 15.2, 15.3, 15.4) = 0. State 15.1 = 1.
22. Labio-maxillary complex (second variable): State 15 (and 15.1, 15.3, 15.4) = 0. State 15.2 = 1.
23. Labio-maxillary complex (third variable): State 15 (and 15.1, 15.2, 15.4) = 0. State 15.3 = 1.
24. Labio-maxillary complex (fourth variable): State 15 (and 15.1, 15.2, 15.3) = 0. State 15.4 = 1.
25. Maxillary palpus (first variable): State 16 (and 16.2) = 0. [State 16.1 = 1; Plumariidae female and within other taxa.]
26. Maxillary palpus (second variable): State 16 (and 16.1) = 0. State 16.2 = 1.
27. Labial palpus: State 17 = 0. State 17.1 = 1.
28. Hind margin of pronotum (first variable): State 18 (and 18.2) = 0. State 18.1 = 1.
29. Hind margin of pronotum (second variable): State 18 (and 18.1) = 0. State 18.2 = 1.
30. Pronotal articulation: State 19 = 0. State 19.1 = 1.
31. Pronotal collar: State 20 = 0. State 20.1 = 1.
32. Posterolateral angle of pronotum (first variable): State 21 (and 21.2, 21.2.1, 21.3) = 0. State 21.1 = 1. State 21.1.1 = 2. State 21.1.1.1 = 3.
33. Posterolateral angle of pronotum (second variable): State 21 (and 21.1, 21.1.1, 21.1.1.1, 21.3) = 0. State 21.2 = 1. State 21.2.1 = 2.
34. Posterolateral angle of pronotum (third variable): State 21 (and all others except 21.3) = 0. State 21.3 = 1.
35. Posteroventral margin of pronotum: State 22 = 0. State 22.1 = 1.
36. Ventral angle of pronotum (first variable): State 23 (and 23.2) = 0. State 23.1 = 1.
37. Ventral angle of pronotum (second variable): State 23 (and 23.1) = 0. State 23.2 = 1.
38. Propleural separation (first variable): State 24 (and 24.2) = 0. State 24.1 = 1.
39. Propleural separation (second variable): State 24 (and 24.1) = 0. State 24.2 = 1.
40. Prosternum: State 25 = 0. State 25.1 = 1. State 25.1.1 = 2.
41. Forecoxal contiguity (first variable): State 26 (and 26.2) = 0. State 26.1 = 1.
42. Forecoxal contiguity (second variable): State 26 (and 26.1) = 0. State 26.2 = 1.
43. Mesonotum: State 27 = 0. State 27.1 = 1.
44. Scutellum: State 28 = 0. State 28.1 = 1. State 28.1.1 = 2.
45. Prepectus (first variable): State 29 (and 29.2) = 0. State 29.1 (and 29.1.2, 29.1.2.1) = 1. State 29.1.1 (and 29.1.1.2, 29.1.1.3) = 2. State 29.1.1.1 = 3.
46. Prepectus (second variable): State 29 (and all others except 29.1.1.2) = 0. State 29.1.1.2 = 1.
47. Prepectus (third variable): State 29 (and all others except 29.1.1.3) = 0. State 29.1.1.3 = 1.

48. Prepectus (fourth variable): State 29 (and all others except 29.1.2, 29.1.2.1) = 0. State 29.1.2 = 1. State 29.1.2.1 = 2.
49. Prepectus (fifth variable): State 29 (and all others except 29.2) = 0. State 29.2 = 1.
50. Mesepimeron (first variable): State 30 (and 30.2) = 0. State 30.1 = 1.
51. Mesepimeron (second variable): State 30 (and 30.1) = 0. State 30.2 = 1.
52. Mesosternum (first variable): State 31 (and 31.2) = 0. State 31.1 = 1. State 31.1.1 = 2.
53. Mesosternum (second variable): State 31 (and 31.1, 31.1.1) = 0. State 31.2 = 1.
54. Mesocoxal contiguity (first variable): State 32 (and 32.2) = 0. State 32.1 = 1.
55. Mesocoxal contiguity (second variable): State 32 (and 32.1) = 0. State 32.2 = 1.
56. Meso-metapleural suture: State 33 = 0. State 33.1 = 1. State 33.1.1 = 2.
57. Metanotum (first variable): State 34 (and 34.2) = 0. State 34.1 = 1.
58. Metanotum (second variable): State 34 (and 34.1) = 0. State 34.2 = 1.
59. Metapostnotum (first variable): State 35 (and 35.2, 35.3) = 0. State 35.1 = 1. State 35.1.1 = 2.
60. Metapostnotum (second variable): State 35 (and 35.1, 35.1.1, 35.3) = 0. State 35.2 = 1.
61. Metapostnotum (third variable): State 35 (and 35.1, 35.1.1, 35.2) = 0. State 35.3 = 1.
62. Metapleuron (first variable): States 36 (and 36.2, 36.3) = 0. State 36.1 (and 36.1.2) = 1. State 36.1.1 = 2.
63. Metapleuron (second variable): State 36 (and all others except 36.1.2) = 0. State 36.1.2 = 1.
64. Metapleuron (third variable): State 36 (and all others except 36.2) = 0. State 36.2 = 1.
65. Metapleuron (fourth variable): State 36 (and all others except 36.3) = 0. State 36.3 = 1.
66. Metapleural gland: State 37 = 0. State 37.1 = 1.
67. Metasternum (first variable): State 38 = 0. State 38.1 = 1. State 38.1.1 (and 38.1.1.2) = 2. State 38.1.1.1 = 3.
68. Metasternum (second variable): State 38 (and 38.1, 38.1.1, 38.1.1.1) = 0. State 38.1.1.2 = 1.
69. Metasternal differentiation: State 39 = 0. State 39.1 = 1.
70. Metasternal anterior production: State 40 = 0. State 40.1 = 1. State 40.1.1 = 2.
71. Metacoxal contiguity: State 41 = 0. State 41.1 = 1.
72. Metathoracic-propodeal pleural suture: State 42 = 0. State 42.1 = 1. State 42.1.1 = 2.
73. Propodeal length: State 43 = 0. State 43.1 = 1.
74. Discal distinction: State 44 = 0. State 44.1 = 1.
75. Extent of forewing venation: State 45 = 0. State 45.1 = 1. State 45.1.1 = 2.
76. Cells of forewing (first variable): State 46 (and 46.2, 46.3, 46.4, 46.5, 46.5.1) = 0. State 46.1 = 1. State 46.1.1 = 2. State 46.1.1.1 = 3.
77. Cells of forewing (second variable): State 46 (and all others except 46.2) = 0. State 46.2 = 1.
78. Cells of forewing (third variable): State 46 (and all others except 46.3) = 0. State 46.3 = 1.
79. Cells of forewing (fourth variable): State 46 (and all others except 46.4) = 0. State 46.4 = 1.
80. Cells of forewing (fifth variable): State 46 (and all others except 46.5 and 46.5.1) = 0. State 46.5 = 1. State 46.5.1 = 2.
81. Pterostigmal size: State 47 = 0. State 47.1 = 1. State 47.1.1 = 2.
82. Pterostigmal sclerotization: State 48 = 0. State 48.1 = 1.
83. Extent of hindwing venation: State 49 = 0. State 49.1 = 1. State 49.1.1 = 2.
84. Cells of hindwing (first variable): State 50 (and 50.2, 50.3, 50.3.1) = 0. State 50.1 = 1.
85. Cells of hindwing (second variable): State 50 (and 50.1, 50.3, 50.3.1) = 0. State 50.2 = 1.
86. Cells of hindwing (third variable): State 50 (and 50.1, 50.2) = 0. State 50.3 = 1. State 50.3.1 = 2.
87. Hindwing anal and jugal veins (first variable): State 51 (and 51.2) = 0. State 51.1 = 1.
88. Hindwing anal and jugal veins (second variable): State 51 (and 51.1) = 0. State 51.2 = 1.
89. Hindwing cross-vein cu-e: State 52 = 0. State 52.1 = 1.
90. Hindwing vein Cu: State 53 = 0. State 53.1 = 1.
91. Basal hamuli (first variable): State 54 (and 54.2) = 0. State 54.1 = 1.

92. Basal hamuli (second variable): State 54 (and 54.1) = 0. State 54.2 = 1.
93. Plical lobe: State 55 = 0. State 55.1 = 1. State 55.1.1 = 2.
94. Jugal lobe (first variable): State 56 (and 56.2) = 0. State 56.1 = 1. State 56.1.1 = 2.
95. Jugal lobe (second variable): State 56 (and 56.1, 56.1.1) = 0. State 56.2 = 1.
96. Leg form (first variable): State 57 (and 57.2, 57.3) = 0. State 57.1 = 1.
97. Leg form (second variable): State 57 (and 57.1, 57.3) = 0. State 57.2 = 1.
98. Leg form (third variable): State 57 (and 57.1, 57.2) = 0. State 57.3 = 1.
99. Arolium: State 58 = 0. State 58.1 = 1.
100. Claws: State 59 = 0. State 59.1 = 1.
101. Foretibial calcar (first variable): States 60 (and 60.2) = 0. State 60.1 = 1. State 60.1.1 = 2.
102. Foretibial calcar (second variable): State 60 (and 60.1, 60.1.1) = 0. State 60.2 = 1.
103. Midtibial spines (first variable): State 61 (and 61.2) = 0. State 61.1 (and 61.1.2) = 1. State 61.1.1 = 2. State 61.1.1.1 = 3. State 61.1.1.1.1 = 4.
104. Midtibial spines (second variable): State 61 (and all others) except 61.1.2 = 0. State 61.1.2 = 1.
105. Midtibial spines (third variable): State 61 (and all others) except 61.2 = 0. State 61.2 = 1.
106. Hindtibial spines (first variable): State 62 (and 62.2) = 0. State 62.1 (and 62.1.2) = 1. State 62.1.1 = 2. State 62.1.1.1 = 3. State 62.1.1.1.1 = 4.
107. Hindtibial spines (second variable): State 62 (and all others except 62.1.2) = 0. State 62.1.2 = 1.
108. Hindtibial spines (third variable): State 62 (and all others except 62.2) = 0. State 62.2 = 1.
109. Midtibial spur number (first variable): State 63 (and 63.2) = 0. State 63.1 = 1.
110. Midtibial spur number (second variable): State 63 (and 63.1) = 0. State 63.2 = 1.
111. Basic form of mid and hindtibial spurs (first variable): State 64 = 0. State 64.1 (and 64.1.2, 64.1.2.1, 64.1.2.1.1) = 1. State 64.1.1 = 2.
112. Basic form of mid and hindtibial spurs (second variable): State 64 (and 64.1, 64.1.1) = 0. State 64.1.2 = 1. [State 64.1.2.1 = 2, *Bradynobaeninae* male only is precursor to state 3]. State 64.1.2.1.1 = 3.
113. Midtibial calcar (first variable): State 65 (and 65.2) = 0. State 65.1 = 1.
114. Midtibial calcar (second variable): State 65 (and 65.1) = 0. State 65.2 = 1.
115. Form of hindcoxa: State 66 = 0. State 66.1 = 1. State 66.1.1 = 2.
116. Hindtibial spur number: State 67 = 0. State 67.1 = 1.
117. Hindtibial calcar (first variable): State 68 (and 68.2, 68.3, 68.4) = 0. State 68.1 = 1.
118. Hindtibial calcar (second variable): State 68 (and 68.1, 68.3, 68.4) = 0. State 68.2 = 1.
119. Hindtibial calcar (third variable): State 68 (and 68.1, 68.2, 68.4) = 0. State 68.3 = 1.
120. Hindtibial calcar (fourth variable): State 68 (and 68.1, 68.2, 68.3) = 0. State 68.4 = 1.
121. Modified mesosoma of apterous female (first variable): State 69 (and 69.2, 69.2.1, 69.2.2, 69.3, 69.3.1, 69.3.2, 69.4) = 0. State 69.1 = 1. State 69.1.1 = 2. State 69.1.1.1 = 3.
122. Modified mesosoma of apterous female (second variable): State 69 (and 69.1, 69.1.1, 69.1.1.1, 69.3, 69.3.1, 69.3.2, 69.4) = 0. State 69.2 (and 69.2.2) = 1. State 69.2.1 = 2.
123. Modified mesosoma of apterous female (third variable): State 69 (and all others except 69.2.2) = 0. State 69.2.2 = 1.
124. Modified mesosoma of apterous female (fourth variable): State 69 (and 69.1, 69.1.1, 69.1.1.1, 69.2, 69.2.1, 69.2.2, 69.4) = 0. State 69.3 (and 69.3.2) = 1. State 69.3.1 = 2.
125. Modified mesosoma of apterous female (fifth variable): State 69 (and all others except 69.3.2) = 0. State 69.3.2 = 1.
126. Modified mesosoma of apterous female (sixth variable): State 69 (and all others except 69.4) = 0. State 69.4 = 1.
127. 'Felt lines' (first variable): State 70 (and 70.2, 70.2.1) = 0. State 70.1 = 1.
128. 'Felt lines' (second variable): State 70 (and 70.1) = 0. State 70.2 = 1. State 70.2.1 = 2.
129. Stridulitra (first variable): State 71 (and 71.2) = 0. State 71.1 = 1.

130. Stridulitra (second variable): State 71 (and 71.1) = 0. State 71.2 = 1.
131. Constriction of metasomal tergumI: State 72 = 0. State 72.1 = 1. State 72.1.1 = 2.
132. Metasomal petiole: State 73 = 0. State 73.1 = 1.
133. Lateral margin of metasomal tergumI: State 74 = 0. State 74.1 = 1. State 74.1.1 = 2.
134. Width of metasomal tergumI: State 75 = 0. State 75.1 = 1. State 75.1.1 = 2.
135. Differentiation of metasomal sternumI: State 76 = 0. State 76.1 = 1.
136. Constriction of second metasomal segment: State 77 = 0. State 77.1 = 1.
137. Metasomal tergumVII of female: State 78 = 0. State 78.1 = 1. State 78.1.1 = 2.
138. Gonocoxite IX of female: State 79 = 0. State 79.1 = 1.
139. GonapophysisVIII of female: State 80 = 0. State 80.1 = 1.
140. Gonapophysis IX of female (first variable): State 81 (and 81.2) = 0. State 81.1 = 1.
141. Gonapophysis IX of female (second variable): State 81 (and 81.1) = 0. State 81.2 = 1.
142. Metasomal sternumVII of male: State 82 = 0. State 82.1 = 1. State 82.1.1 = 2.
143. Form of male hypopygium (first variable): All states except 83.1 = 0. State 83.1 = 1.
144. Form of male hypopygium (second variable): All states except 83.2 = 0. State 83.2 = 1.
145. Form of male hypopygium (third variable): All states except 83.3 = 0. State 83.3 = 1.
146. Form of male hypopygium (fourth variable): State 83 (and 83.1, 83.2, 83.3) = 0. State 83.4 = 1. State 83.4.1 = 2.
147. Concealment of male hypopygium (first variable): State 84 (and 84.2) = 0. State 84.1 = 1.
148. Concealment of male hypopygium (second variable): State 84 (and 84.1) = 0. State 84.2 = 1.
149. Cercus of male: State 85 = 0. State 85.1 = 1.
150. GonapophysisIX of male (first variable): State 86 (and 86.2) = 0. State 86.1 = 1.
151. Gonapophysis IX of male (second variable): State 86 (and 86.1) = 0. State 86.2 = 1.
152. Larval mandibular teeth (first variable): State 87 (and 87.2, 87.3) = 0. State 87.1 = 1.
153. Larval mandibular teeth (second variable): State 87 (and 87.1, 87.3) = 0. State 87.2 = 1.
154. Larval mandibular teeth (third variable): State 87 (and 87.1, 87.2) = 0. State 87.3 = 1.
155. Larval spiracles: State 88 = 0. State 88.1 = 1.
156. Number of prey: State 89 = 0. State 89.1 = 1.
157. Nest construction (first variable): State 90 (and 90.2) = 0. State 90.1 (and 90.1.2, 90.1.3) = 1. State 90.1.1 = 2.
158. Nest construction (second variable): State 90 (and 90.1, 90.1.3, 90.2) = 0. State 90.1.2 = 1.
159. Nest construction (third variable): State 90 (and 90.1, 90.1.2, 90.2) = 0. State 90.1.3 = 1.
160. Nest construction (fourth variable): State 90 (and 90.1, 90.1.2, 90.1.3) = 0. State 90.2 = 1.
161. Oviposition sequence: State 91 = 0. State 91.1 = 1.
162. Type of provisions: State 92 = 0. State 92.1 = 1.

APPENDIX V

Distribution of derived character states on preferred cladogram (see text) of Aculeata (Fig. 8b) resulting from analysis of data from Brothers (1975) (Table III); optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 72 and 83. Unnamed internodes are referred to by listing the subtended superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix IV; transformations are denoted by listing the ancestral and derived states separated by a ">".

Final weights of variables (10 is maximum):

Weight = 10: 1, 3, 5, 6, 9, 10, 17, 18, 20, 21, 22, 23, 24, 25, 26, 29, 30, 31, 33, 34, 37, 38, 39, 40, 41, 42, 44, 46, 47, 49, 55, 58, 60, 61, 63, 65, 66, 68, 70, 71, 77, 78, 79, 80, 85, 86, 87, 89, 90, 97, 98, 101, 102, 104, 105, 107, 108, 110, 112, 113, 114, 116, 118, 119, 120, 122, 123, 124, 125, 126, 127, 128, 129, 132, 133, 134, 136, 137, 138, 143, 144, 145, 146, 150, 151, 154, 158, 159, 162

Weight = 6: 45

Weight = 5: 48, 94

Weight = 4: 7, 36, 51, 155

Weight = 3: 19, 52, 53, 59, 67, 76, 131, 152

Weight = 2: 4, 8, 15, 16, 32, 43, 56, 57, 62, 69, 81, 88, 99, 103, 106, 111, 130, 135, 140, 141, 157, 160

Weight = 1: 28, 74, 75, 82, 83, 92, 93, 95, 96, 115, 149

Weight = 0: 2, 11, 12, 13, 14, 27, 35, 50, 54, 64, 72, 73, 84, 91, 100, 109, 117, 121, 139, 142, 147, 148, 153, 156, 161

(Aculeata): 40:0>1, 75:0>1, 103:0>1, 106:0>1

(Plumariidae, bethylids, Scolebythidae): 72:0>1, 76:0>1, 88:0>1, 95:0>1, 138:0>1

Plumariidae: 2:0>1, 16:0>1, 39:0>1, 67:0>1, 96:0>1, 126:0>1, 139:0>1, 142:0>1

(bethylids, Scolebythidae): 40:1>0, 60:0>1, 76:1>2, 83:0>1, 86:0>1, 103:1>0, 106:1>0

bethylids ('higher' Chrysidoidea): 27:0>1

Scolebythidae: 5:0>1, 11:0>1, 13:0>1, 31:0>1, 42:0>1, 58:0>1, 76:2>3, 83:1>2, 86:1>2, 97:0>1, 105:0>1, 108:0>1

(Apoidea, Vespoidea): 18:0>1, 35:0>1, 41:0>1, 81:0>1, 137:0>1

(Apoidea): 29:0>1, 33:0>1, 37:0>1, 43:0>1, 49:0>1, 53:0>1, 56:0>1, 61:0>1, 65:0>1, 69:0>1, 111:0>2, 141:0>1, 157:0>1

sphecids (Sphecidae s.l.): 33:1>2, 75:1>0, 103:1>2, 106:1>2

apids (Apidae s.l.): 4:0>1, 21:0>1, 51:0>1, 72:0>1, 84:0>1, 87:0>1, 109:0>1, 137:1>2, 142:0>2, 148:0>1, 149:0>1, 153:0>1, 156:0>1, 157:1>2, 162:0>1

(Vespoidea): 13:0>1, 38:0>1, 45:0>1, 52:0>1, 64:0>1, 67:0>2, 84:0>1, 88:0>1, 93:0>1

Sierolomorphidae: 72:0>1, 77:0>1, 81:1>0, 83:0>1, 95:0>1, 115:0>1, 143:0>1, 148:0>1

(Rhopalosomatidae, Scolidae, Vespidae, Formicidae, Bradynobaenidae, Pompilidae, Sapygidae, Mutillidae, Tiphidae): 82:0>1, 94:0>1, 142:0>1

(Rhopalosomatidae, Scolidae, Vespidae, Formicidae, Bradynobaenidae): 28:0>1, 32:0>1, 43:0>1, 45:1>2, 131:0>1, 141:0>1

Rhopalosomatidae: 52:1>2, 54:0>1, 76:0>1, 83:0>1, 91:0>1, 93:1>0, 98:0>1, 117:0>1, 154:0>1

(Scolidae, Vespidae, Formicidae, Bradynobaenidae): 36:0>1, 52:1>0, 56:0>1, 59:0>2, 62:0>1, 64:1>0, 135:0>1, 152:0>1, 156:0>1, 157:0>1

(Scolidae, Vespidae): 6:0>1, 10:0>1, 13:1>0, 22:0>1, 30:0>1, 32:1>2, 40:1>2, 53:0>1, 84:1>0, 92:0>1, 141:1>0, 149:0>1

Scolidae: 15:0>1, 46:0>1, 50:0>1, 55:0>1, 63:0>1, 68:0>1, 69:0>1, 71:0>1, 74:0>1, 83:0>1, 93:1>2, 96:0>1, 100:0>1, 102:0>1, 104:0>1, 107:0>1,

109:0>1, 111:1>2, 142:1>0, 144:0>1, 148:0>1, 150:0>1, 156:0>1

Vespidae: 32:2>3, 45:2>3, 54:0>1, 73:0>1, 75:1>0, 118:0>1, 131:1>0, 139:0>1, 157:1>2, 161:0>1

(Formicidae, Bradynobaenidae): 51:0>1, 82:1>0, 103:1>2, 106:1>3, 132:0>1, 161:0>1

Formicidae: 3:0>1, 47:0>1, 56:1>2, 66:0>1, 75:1>0, 76:0>1, 92:0>1, 103:2>3, 113:0>1, 119:0>1, 142:1>0, 158:0>1

(Bradynobaenidae): 2:0>1, 16:0>1, 28:1>0, 32:1>0, 43:1>0, 67:2>0, 69:0>1, 70:0>1, 72:0>1, 83:0>1, 93:1>2, 124:0>1, 128:0>1, 130:0>1, 133:0>1, 139:0>1

(Typhoctinae): 4:0>1, 35:1>0, 36:1>0, 62:1>0, 64:0>1, 91:0>1, 106:3>2, 115:0>1, 124:1>2

Eotillini: 81:1>0, 93:2>0, 99:0>1, 103:2>1, 106:2>1

Typhoctini: 84:1>0, 94:1>0, 95:0>1

(Chyphotinae, Apterogyninae, Bradynobaeninae): 7:0>1, 9:0>1, 12:0>1, 13:1>0, 19:0>1, 96:0>1, 125:0>1, 133:1>2, 134:0>1, 146:0>1

Chyphotinae: 56:1>2, 81:1>0, 91:0>1, 134:1>2, 147:0>1

(Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 44:0>1, 57:0>1, 70:1>2, 75:1>2, 80:0>1, 81:0>2, 83:1>2, 84:1>0, 92:0>1, 99:0>1, 101:0>1, 103:2>3, 111:0>1, 112:0>1, 130:1>0, 149:0>1

Apterogyninae: 115:0>1, 131:1>2, 136:0>1, 139:1>0

Bradynobaeninae: 8:0>1, 12:1>0, 24:0>1, 26:0>1, 27:0>1, 34:0>1, 44:1>2, 62:1>2, 73:0>1, 74:0>1, 80:1>2, 85:0>1, 100:0>1, 101:1>2, 103:3>4, 106:3>4, 110:0>1, 112:1>3, 128:1>2, 140:0>1, 141:1>0, 146:1>2

(Pompilidae, Sapygidae, Mutillidae, Tiphidae): 13:1>0, 75:1>0, 103:1>2, 106:1>2, 155:0>1

Pompilidae: 48:0>1, 54:0>1, 56:0>1, 91:0>1, 111:0>1, 117:0>1, 139:0>1, 152:0>1, 159:0>1

(Sapygidae, Mutillidae, Tiphidae): 35:1>0, 59:0>1, 64:1>0, 81:1>0, 82:1>0, 89:0>1, 115:0>1

(Sapygidae, Mutillidae): 7:0>1, 48:0>1, 90:0>1, 94:1>2, 151:0>1

Sapygidae: 23:0>1, 139:0>1, 153:0>1, 155:1>0

(Mutillidae): 2:0>1, 19:0>1, 20:0>1, 48:1>2, 54:0>1, 62:0>1, 72:0>2, 91:0>1, 122:0>1, 129:0>1, 135:0>1, 140:0>1, 160:0>1

Myrmosinae: 14:0>1, 115:1>2, 122:1>2, 142:1>0, 148:0>1

mutillids ('higher' Mutillidae): 28:0>1, 32:0>1, 50:0>1, 57:0>1, 67:2>3, 75:0>1, 83:0>1, 123:0>1, 127:0>1 (Tiphidae): 52:1>2, 67:2>1, 84:1>0, 96:0>1

Thynninae (s.l.): 2:0>1, 121:0>1

(Anthoboscinae, Tiphinae, Brachycistidinae, Myzininae, Methochinae): 93:1>0, 115:1>0

Anthoboscinae: 147:0>1

(Tiphinae, Brachycistidinae, Myzininae, Methochinae):
35:0>1, 135:0>1, 140>1, 145:0>1

(Tiphinae, Brachycistidinae): 32:0>1, 56:0>1, 62:0>2,
72:0>1, 74:0>1, 75:0>1, 83:0>1, 115:0>1, 131:0>1,
142:1>2, 148:0>1, 149:0>1

Tiphinae: 59:1>2, 72:1>2, 79:0>1

Brachycistidinae: 2:0>1, 12:0>1, 16:0>1, 45:1>2,
92:0>1, 100:0>1, 109:0>1, 121:0>3

(Myzininae, Methochinae): 1:0>1, 8:0>1, 142:1>0

Myzininae: 35:1>0, 59:1>2, 140:1>0

Methochinae: 2:0>1, 11:0>1, 14:0>1, 52:1>0, 72:0>1,
78:0>1, 84:0>1, 96:1>0, 103:2>1, 106:2>1, 114:0>1,
116:0>1, 120:0>1, 121:0>2, 160:0>1

APPENDIX VI

Variables used in final analyses of Aculeata, based on characters and states from Brothers (1975), Brothers (1976), Rasnitsyn (1980, 1988), Carpenter (1986), Johnson (1988), Kimsey (1991), new interpretations and new characters; all refer to adults unless otherwise specified.

The scores for the taxa are given in Tables IV and V. Characters are treated as additive except as noted. Polarity was conferred by the addition of an all-primitive ancestral taxon to the matrix.

Variables 1-18 and 21-185 are those used to score the 92 characters from Brothers (1975) given in Appendix IV and Table III, except that the following three variables of Appendix IV have been deleted for the reasons stated: 5 (very short clypeus, supposed autapomorphy of *Scolebythidae*, not shown in *Ycaploca*), 29 (U-shaped posterior pronotal margin duplicates Variable 33 of Appendix IV), 58 (much constricted metanotum, supposed autapomorphy of *Scolebythidae*, not shown in *Ycaploca*). New characters are Variables 19-20 and 186-219. The majority of the characters used by Rasnitsyn (1980, 1988) (Appendices II and III) are subsumed in the coding for the characters in Appendix IV, which is based on fuller study (examination of more characters and taxa than done by Rasnitsyn); where the inferred polarities of major features differed between Brothers (1975) and Rasnitsyn (1980, 1988), we have re-evaluated them and sometimes treated the polarity of the states of such characters as nonadditive.

Newly scored taxa (not considered separately by Brothers, 1975) are Bethyilidae, Chrysidae, Sclerogibbidae, Embolemlidae, Dryinidae, Heterogynaidae, Diamminae, Thynninae, *Olixon*, macropterous rhopalosomatids (including *Liosphex*), Proscoliinae, Scolinae, Fedtschenkiinae and Sapyginae; *Scolebythidae* has been rescored to include *Ycaploca*. Other changes of interpretation from those in Appendix IV and the source publications are noted where relevant. In order to permit this new analysis to stand on its own, all variables and states are specified here, including those which are unchanged from Brothers's (1975) treatment, but the descriptions are shorter and often differ for greater clarity or as a result of the different system of coding used; because of the consideration of more taxa, new states have been added to some characters. To aid comparison, the equivalent characters in Brothers (1975) (C) and variables in Appendix IV (above) (V) are specified. The terminology of Brothers (1975) has been maintained for consistency, although different terminology for some features (e.g., wing veins) has been more generally adopted since that paper. Sexually dimorphic states used by Brothers (1975) but not included in this analysis (see text), are indicated by comments.

Variables considered unlikely to show reversals: 2, 15, 16, 27-29, 31, 32, 48 (State 3), 49-53, 61 (State 2), 77, 80 (State 2), 81 (State 2), 84-92, 95-102, 104-106, 109, 113, 124, 125, 131, 137-144, 151 (State 2), 152, 153, 156, 157, 161, 171, 178, 196, 198, 201, 202, 204, 215, 216 (State 2).

1. Sexual dimorphism in body proportions: None or slight although dimorphism in wing development may be considerable = 0. Male very much more slender than female = 1. (C1, V1)
2. Sexual dimorphism in wing development: Both sexes fully winged or equally brachypterous = 0. Male macropterous and female strongly brachypterous or apterous = 1. (C2) [Modification of V2 to account for conditions in *Olixon* and *Heterogynaidae*.]
3. Sterile caste: All females fertile = 0. Some females sterile and forming specialized caste = 1. (C3, V3)

4. Pubescence: Simple = 0. Some plumose = 1. (C4, V4)
5. Clypeus height: Moderate (or very short) = 0. Dorsally produced = 1. (C5, V6)
6. Antennal socket (first variable): Rim simple (or frontal ledge present) = 0. Rim produced dorsally to form differentiated 'tubercle' = 1. (C6, V7)
7. Antennal socket (second variable): Rim simple (or modified differently from State 1) = 0. Frons expanded as frontal ledge overhanging anteriorly-facing socket = 1. (C6, V8)
8. Antennal socket (third variable): Rim simple (or modified differently from State 1) = 0. Frons and socket produced as frontal ledge with ventrally-facing socket = 1. (C6) [Addition of variable for condition in Sclerogibbidae.]
9. Compound eye form (first variable): Oval with inner margin shallowly sinuate (or inner margin emarginate or convex) = 0. Rounded with inner margin shallowly sinuate = 1. [State 2, Chyphotinae and Apterygyninae females only, deleted.] (C7, V9)
10. Compound eye form (second variable): Oval (or rounded) with inner margin shallowly sinuate (or convex) = 0. Oval with inner margin emarginate = 1. (C7, V10)
11. Compound eye form (third variable): Oval with inner margin shallowly sinuate (or emarginate, or eye rounded) = 0. Oval with inner margin convex = 1. (C7, V11)
12. Compound eye contour: Following general contours of head = 0. Highly differentiated, eye protuberant = 1. (C8, V12)
13. Compound eye pores and setae (first variable): Scattered pores with setae minute (or long, or no pores or setae) = 0. Scattered pores with short setae = 1. Dense pores with short setae = 2. (C9, V13) [Addition of state for condition in Sclerogibbidae.]
14. Compound eye pores and setae (second variable): Pores with setae minute (or short, or no pores or setae) = 0. Scattered pores with long setae = 1. (C9, V14)
15. Compound eye pores and setae (third variable): Present = 0. Absent = 1. (C9, V15)
16. Ocelli: Present in both sexes = 0. Absent in one or both sexes = 1. (C10, V16)
17. Genal organ: Absent = 0. Present = 1. (C11, V17)
18. Sexual dimorphism in antennomere number: None = 0. Male with 13 and female with 12 antennomeres = 1. (C12, V18)
19. Antennomere number (first variable): Fewer than 14 antennomeres = 0. More than 14 antennomeres = 1.
20. Antennomere number (second variable): More than 11 antennomeres = 0. Ten antennomeres = 1.
(Variables 19-20: new character for conditions in various Chrysidoidea; see Carpenter (1986).]
21. Radicle axis: Scape and radicle sharing a common axis = 0. Axis of radicle at a distinct angle to that of scape = 1. (C13, V19)
22. Radicle-scape insertion: Simple annular constriction = 0. Radicle inserted under flangelike expansion of scape = 1. (C14, V20)
23. Labio-maxillary complex (first variable): Short and adapted for lapping (or modified differently from States 1 and 2) = 0. Elongated by production of prementum and stipes only = 1. Elongated by production of prementum and stipes and of glossa = 2. (C15, V21 & V23)
24. Labio-maxillary complex (second variable): Short and adapted for lapping (or modified differently from State 1) = 0. Elongated by production of glossa and paraglossa only = 1. (C15, V22)
25. Labio-maxillary complex (third variable): Short and adapted for lapping (or modified differently from State 1) = 0. Elongated by production of prementum and stipes but glossa and paraglossa much reduced = 1. (C15)
26. Labio-maxillary complex (fourth variable): Short and adapted for lapping (or elongated) = 0. Much reduced = 1. (C15, V24)
[Variables 23-26: modification of C15 to reflect conditions in Fedtschenkiinae and Apyginae more accurately.]

27. Maxillary palpus (first variable): Six- (or two-) segmented = 0. Five-segmented = 1. (C16, V25)
28. Maxillary palpus (second variable): Six- (or five-) segmented = 0. Two-segmented = 1. (C16, V26)
29. Labial palpus: Four-segmented = 0. Three-segmented = 1. (C17, V27)
30. Posterior margin of pronotum (first variable): Nearly straight, shallowly evenly concave or broadly U-shaped = 0. V-shaped, pronotum shortened medially = 1. (C18, V28)
31. Pronotal articulation (first variable): Pronotum freely articulating with mesothorax (or pronotum fused with prepectus and closely abutting mesepisternum) = 0. Pronotum closely abutting prepectus which fused with mesepisternum = 1. (C19)
32. Pronotal articulation (second variable): Pronotum freely articulating with mesothorax (or pronotum closely abutting prepectus which fused with mesepisternum) = 0. Pronotum fused with hidden prepectus and closely abutting mesepisternum = 1. Pronotum fused with large exposed prepectus which closely abutting mesepisternum = 2. NONADDITIVE (C19)
[Variables 31-32: addition of variable to differentiate between separate derivations of immovable pronotum in scoliids and vespids, see Gibson (1985:1417); and for condition in Embolemidae.]
33. Anterior collar of pronotum: Present and concealing anteriorly separated propleura from above = 0. Absent or greatly reduced and exposing anteriorly contiguous propleura from above = 1. (C20, V31)
34. Posterolateral angle of pronotum (first variable): Evenly rounded and reaching tegula (or modified differently from States 1, 2 or 3) = 0. Slightly dorsally produced, truncate and reaching tegula = 1. Dorsally produced, notched and slightly exceeding anterior margin of tegula = 2. Dorsally produced, acute and much exceeding anterior margin of tegula = 3. (C21, V32)
35. Posterolateral angle of pronotum (second variable): Evenly rounded and reaching tegula (or modified differently from State 1) = 0. Reduced dorsally above and anterior to differentiated spiracular operculum and reaching tegula = 1. [State 2, supposed autapomorphy of sphecid, deleted since not shown in Dolichurini] (C21, V33)
36. Posterolateral angle of pronotum (third variable): Evenly rounded and reaching tegula (or modified differently from State 1) = 0. Posteriorly produced below tegula = 1. (C21, V34)
37. Posteroventral margin of pronotum: Approximately straight = 0. Distinctly concave = 1. (C22, V35)
38. Ventral angle of pronotum (first variable): Broadly rounded and scarcely exceeding base of procoxa (or produced mesad and approaching its counterpart midventrally) = 0. Very narrowly rounded and slightly produced ventrally beyond base of procoxa and lateral to it = 1. Acute and produced ventrally beyond base of procoxa and lateral to it = 2. (C23, V36)
39. Ventral angle of pronotum (second variable): Scarcely exceeding base of procoxa (or produced ventrally beyond base of procoxa and lateral to it) = 0. Greatly produced mesad and approaching its counterpart midventrally although well separated from it = 1. Greatly produced mesad and closely approaching its counterpart midventrally = 2. (C23, V37)
[Variables 38-39: reformulation and addition of intermediate states as found in Proscoliinae and Heterogynaidae.]
40. Propleural separation (first variable): Propleura separated posteriorly = 0. Propleura mesally contiguous posteriorly with posterior margins forming more or less straight line = 1. (C24, V38)
41. Propleural separation (second variable): Propleura separated and exposing medial membranous areas anterodorsally = 0. Propleura contiguous or fused over some distance anterodorsally, forming short tubular necklike region = 1. (C24) [New variable, reformulation of V39 to avoid overlap with V144.]

42. Propleural separation (third variable): Propleura narrowly separated or contiguous posteriorly = 0. Propleura very widely separated posteriorly and exposing enlarged prosternum = 1. (C24) [Addition of extreme state for condition in Scolebythidae, see Carpenter (1986).]
43. Prosternum: Forming an even plane and not sunken except at most for very short region posteriorly = 0. Forming different planes and sunken except for short region anteriorly = 1. Entirely sunken = 2. (C25, V40)
44. Procoxal contiguity: Somewhat separated basally by broad prosternum = 0. Contiguous basally through reduction in prosternum = 1. (C26, V41)
45. Protochanteral insertion: Apical on coxa = 0. Near base of coxa = 1. (C26, V42)
[Variables 44-45: reformulation of V41 and V42 as separate characters.]
46. Mesonotum: Scarcely extending anterior to tegulae = 0. Extending far anterior to tegulae = 1. (C27, V43)
47. Scutellum: Flattened and poorly differentiated = 0. Posterodorsally swollen and protuberant = 1. Posterodorsally produced and overhanging metanotum = 2. (C28, V44)
48. Prepectus (first variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or halves fused midventrally) = 0. Free with each half narrowed and widely separated from its counterpart = 1. Each half narrowed and shortened as a small elongate strip articulating with (or fused to) anterior margin of mesepisternum = 2. Each half very narrow and short, extending over dorsal half or less of mesepisternum, fused with pronotum and concealed under its posterolateral angle = 3. (C29, V45) [Reformulation to include reinterpretation of condition in Vespidae, see Gibson (1985).]
49. Prepectus (second variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Each half very narrow and short, extending over less than dorsal half of mesepisternum, fused with mesepisternum and concealed under posterolateral angle of pronotum = 1. (C29, V46)
50. Prepectus (third variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Each half very short but extending over most of height of mesepisternum, fused with mesepisternum and concealed under posteroventral margin of pronotum = 1. (C29, V47)
51. Prepectus (fourth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from States 1 and 2) = 0. Not shortened, extending over most of height of mesepisternum and fused with it, line of fusion forming distinct sulcus = 1. Not shortened, extending over most of height of mesepisternum and fused with it, line of fusion obliterated except at two ventral pits = 2. (C29, V48)
52. Prepectus (fifth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from State 1) = 0. Transverse with halves fused midventrally and to meso-pleurosternum = 1. (C29, V49)
53. Prepectus (sixth variable): Transverse and free, divided midventrally with halves contiguous and articulating with mesopleurosternum (or modified differently from States 1 and 2) = 0. Transverse with halves fused midventrally but not fused with mesopleurosternum = 1. Transverse with halves fused midventrally, fused with pronotum but not fused with mesopleurosternum = 2. NONADDITIVE (C29) [Addition of variable for conditions in some Chrysidoidea.]
54. Mesepimeron (first variable): Extending full height of mesopleuron and differentiated by complete pleural sulcus (or modified differently from State 1) = 0. Extending full height of mesopleuron and differentiated only dorsally by pleural sulcus = 1. (C30, V50)

55. Mesepimeron (second variable): Extending full height of mesopleuron = 0. Restricted to dorsal half of mesopleuron with pleural sulcus coincident with meso-metapleural suture ventrally = 1. (C30, V51)
56. Mesosternum (first variable): Smoothly truncate posteriorly = 0. With short transverse carina or weak tooth anteromesal to mesocoxal cavity = 1. With lamella anteromesal to mesocoxal cavity and projecting over it = 2. (C31, V52)
57. Mesosternum (second variable): Not posteriorly produced mesally = 0. Posteromesally produced and carrying mesal articulations of mesocoxae = 1. Posteromesally acutely produced without affecting mesal articulations of mesocoxae = 2. (C31, V53) NON-ADDITIVE [Reformulation to account for condition in some Chrysidoidea.]
58. Mesocoxal contiguity (first variable): Mesocoxae slightly (or widely) separated basally = 0. Mesocoxae contiguous as result of reduction in intercoxal region of mesosternum = 1. (C32, V54)
59. Mesocoxal contiguity (second variable): Mesocoxae slightly separated basally (or modified differently from State 1) = 0. Mesocoxae widely separated as a result of lateral expansion without shortening of intercoxal region of mesosternum = 1. (C32)
60. Mesocoxal contiguity (third variable): Mesocoxae slightly separated basally (or modified differently from State 1) = 0. Mesocoxae very widely separated as a result of lateral expansion and shortening of intercoxal region of mesosternum = 1. (C32)
[Variables 59-60: reformulation of V55 and addition of new variable to differentiate between apparently independent processes causing separation of mesocoxae in Scolidae and some Bradynobaenidae.]
61. Meso-metapleural suture: Freely articulating = 0. Immovable but not fused = 1. Entirely or only dorsally fused although distinct = 2. (C33, V56)
62. Metanotum: About as long laterally as mesally = 0. Nearly twice as long laterally as mesally = 1. (C34, V57)
63. Metapostnotum (first variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or modified differently from States 1 and 2) = 0. Partially invaginated and barely visible mesally between metanotum and propodeum = 1. Invaginated and not visible mesally between metanotum and propodeum = 2. (C35, V59)
64. Metapostnotum (second variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or modified differently from States 1, 2 or 3) = 0. Transverse, visible mesally and not invaginated, depressed with posterior margin indistinct mesally = 1. Transverse, very much shortened and hidden mesally but not invaginated, depressed with posterior margin indistinct = 2. (C35, V60) [Addition of state and reformulation to describe conditions in Chrysidoidea more accurately; Carpenter (1986) corrected.]
65. Metapostnotum (third variable): Transverse, depressed and distinct mesally between metanotum and propodeum (or shortened) = 0. Strongly expanded posteromesally to form 'propodeal triangle' = 1. (C35, V61)
66. Metapleuron of macropterous form (first variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from States 1 and 2) = 0. With anterodorsal part of pleural sulcus curved (or angled) and only partly coincident with meso-metapleural suture, posteroventral part convex or straight (or strongly concave) and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and some distance posterior to straightish meso-metapleural suture at or above mid-height = 1. With anterodorsal part of pleural sulcus curved and partly coincident with

- meso-metapleural suture, posteroventral part convex and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to posteriorly convex meso-metapleural suture at or above mid-height = 2. (C36)
67. Metapleuron of macropterous form (second variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus curved and partly coincident with meso-metapleural suture, posteroventral part strongly concave and coincident with metapleural-propodeal suture and passing through ventral pit; true endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and some distance posterior to straightish meso-metapleural suture at or above mid-height = 1. (C36)
68. Metapleuron of macropterous form (third variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus almost entirely coincident with meso-metapleural suture but extended anteroventral to endophragmal pit, posteroventral part curved and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture slightly below mid-height = 1. (C36)
69. Metapleuron of macropterous form (fourth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part angled and coincident with metapleural-propodeal suture only posteroventrally; endophragmal pit within pleural sulcus and close to straightish meso-metapleural suture at about mid-height = 1. (C36)
70. Metapleuron of macropterous form (fifth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture, endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus coincident with meso-metapleural suture only anterodorsally but extended anteroventral to endophragmal pit and angled, posteroventral part angled and coincident with metapleural-propodeal suture only posteroventrally; endophragmal pit within pleural sulcus and some distance posterior to straightish meso-metapleural suture at about mid-height = 1. (C36)
71. Metapleuron of macropterous form (sixth variable): With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part convex or straight and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture

at or above mid-height (or modified differently from State 1) = 0. With anterodorsal part of pleural sulcus straightish and almost entirely coincident with meso-metapleural suture, posteroventral part straight or weakly concave and coincident with metapleural-propodeal suture; endophragmal pit at juncture of pleural sulcus and metapleural-propodeal suture and close to straightish meso-metapleural suture below mid-height = 1. (C36)

[Variables 66-71: total re-evaluation and recoding consequential on observation of conditions in taxa not examined by Brothers (1975) and different interpretations, see Rasnitsyn (1980).]

72. Metapleural gland: Absent = 0. Present = 1. (C37, V66)

73. Metasternum (first variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from States 1 and 2) = 0. Entirely depressed without teeth (or with separated small teeth just anterior to metacoxal cavities, or depressed only laterally) and mesocoxae more or less contiguous = 1. Entirely depressed with medially fused small teeth just anterior to metacoxal cavities and mesocoxae contiguous = 2. (C38)

74. Metasternum (second variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from States 1 and 2) = 0. Entirely depressed with separated small teeth just anterior to metacoxal cavities and mesocoxae contiguous = 1. Depressed only laterally and mesocoxae more or less contiguous = 2. (C38)

75. Metasternum (third variable): Depressed anterolaterally but not medially nor posteriorly (or modified differently from State 1) = 0. Depressed only laterally and mesocoxae separated = 1. (C38)

76. Metasternum (fourth variable): Partly or entirely depressed = 0. Broad, not depressed and mesocoxae widely separated = 1. (C38)

[Variables 73-76: reformulation of V67-68 to take new interpretations into account; see Rasnitsyn (1980), Carpenter (1986), Kimsey (1991).]

77. Metasternal differentiation: Meso- and metasterna distinctly differentiated by a deep sulcus or difference in level = 0. Meso- and metasterna scarcely differentiated through fusion and loss of any sulcus, at least mesally = 1. (C39, V69)

78. Metasternal anterior margin: Approximately straight and at a level posterior to anterior extremities of mesocoxae = 0. Slightly anteromesally produced to level of anterior extremities of mesocoxae = 1. Anteromesally produced to level anterior to mesocoxae = 2. (C40, V70)

79. Metacoxal contiguity: Contiguous or nearly so = 0. Broadly separated = 1. (C41, V71)

80. Metathoracic-propodeal pleural suture (first variable): Distinct and complete ventral to endophragmal pit = 0. Reduced but partly discernible ventral to endophragmal pit = 1. Obliterated ventral to endophragmal pit = 2. NONADDITIVE (C42)

81. Metathoracic-propodeal pleural suture (second variable): Distinct and complete dorsal to endophragmal pit = 0. Reduced but partly discernible dorsal to endophragmal pit = 1. Obliterated dorsal to endophragmal pit = 2. NONADDITIVE (C42)

[Variables 80-81: reformulation of V72 and addition of a variable to permit independent losses and intermediate states.]

82. Propodeal length: At least as long as high = 0. Much shorter than high = 1. (C43, V73)

83. Propodeal disc: Merging evenly with declivity = 0. Distinct from declivity = 1. (C44, V74)

84. Extent of forewing venation: Reaching apical margin = 0. Extending into apical half of membrane but not reaching apical margin = 1. Restricted to basal half of membrane = 2. (C45, V75)

85. Closed cells in forewing (first variable): Ten (or modified differently from States 1, 2 and 3) = 0. Eight (C not much reduced) = 1. Seven (C, SC+R+S, SC+R, R, S+M, M+Cu, 1Cu) (or six but unlike State 2) = 2. Six (C, SC+R+S, SC+R, R, S+M, M+Cu) = 3. (C46, V76)

86. Closed cells in forewing (second variable): Ten (or modified differently from State 1) = 0. Six (C, SC+R+S, R, S+M, M+Cu, 1Cu) = 1. Five (C, SC+R+S, R, M+Cu, 1Cu) = 2. (C46)
87. Closed cells in forewing (third variable): Ten (or modified differently from State 1) = 0. Six (C, SC+R+S, SC+R, R (not subdivided), M+Cu, 1Cu) = 1. (C46)
88. Closed cells in forewing (fourth variable): Ten (or modified differently from State 1) = 0. Seven (C, SC+R+S, (SC+R)+1S, R, S+M, M+Cu, 1Cu) = 1. (C46, V77)
89. Closed cells in forewing (fifth variable): Ten (or modified differently from States 1 and 2) = 0. Nine (C, SC+R+S, R, (SC+R)+1S (vein S obliterated just proximal to fusion with vein r-s), 2S, S+M, 1M, M+Cu, 1Cu) = 1. Nine (C, SC+R+S, SC+R, R, 1S, S+M, 1M, M+Cu, 1Cu) = 2. NONADDITIVE (C46)
90. Closed cells in forewing (sixth variable): Ten (or modified differently from States 1 and 2) = 0. Nine (C, SC+R+S, R, (SC+R)+1S (vein S obliterated just distal to separation from vein M), S+M, 1M, M+Cu, 1Cu) = 1. Six (C, SC+R+S, SC+R, R (subdivided), M+Cu, 1Cu) = 2. NONADDITIVE (C46)
91. Closed cells in forewing (seventh variable): Ten (or modified differently from States 1 and 2) = 0. Five (C, SC+R+S, SC+R, M+Cu, 1Cu) = 1. Three (C, SC+R+S, M+Cu) = 2. (C46, V80)
92. Closed cells in forewing (eighth variable): Ten (or modified differently from States 1 and 2) = 0. Eight (C present but almost eliminated through partial fusion of veins C and SC) = 1. Three (probably SC+R+S, SC+R, R; C eliminated) = 2. (C46)
- [Variables 85-92: addition of states and variables for conditions in various Chrysidoidea, Proscoliinae, Heterogynaidae and *Olixon*, see Carpenter (1986) and others; 1Cu considered as a closed cell if vein Cu1 well-developed, even when vein Cu2 reduced or absent and/or vein E apically weakened.]
93. Pterostigmal size: Large and prominent = 0. Medium to small but distinct = 1. Very small and not distinct = 2. (C47, V81)
94. Pterostigmal sclerotization: Complete = 0. Reduced apically, pterostigma partially cell-like = 1. Entirely reduced, pterostigma completely cell-like = 2. (C48, V82) [Addition of intermediate state for condition in Proscoliinae.]
95. Extent of hindwing venation: Reaching apical margin = 0. Extending into apical half of membrane but not reaching apical margin = 1. Restricted to basal half of membrane = 2. (C49, V83)
96. Closed cells in hindwing (first variable): Three (or two (C, (SC+R+S)+(M+Cu)) or none) = 0. Two (SC+R+S, M+Cu) = 1. (C50, V84)
97. Closed cells in hindwing (second variable): Three (or two (SC+R+S, M+Cu) or none) = 0. Two (C, (SC+R+S)+(M+Cu)) = 1. (C50, V85)
98. Closed cells in hindwing (third variable): Three (or two) = 0. One (C, hypothetical intermediate state) (or none but unlike State 2) = 1. None, vein C long, vein SC+R+S absent (vein running along margin and abruptly narrowed at base, weak longitudinal crease in membrane indicating position of separate SC+R+S) = 2. (C50)
99. Closed cells in hindwing (fourth variable): One or more (or none but unlike State 1) = 0. None, veins C and SC+R+S long but fused (vein running along margin and of even broad thickness, no longitudinal crease in membrane indicating separate SC+R+S) = 1. (C50)
100. Closed cells in hindwing (fifth variable): One or more (or none but unlike States 1 and 2) = 0. None, vein C short and vein SC+R+S absent (vein running along margin and weak longitudinal crease in membrane indicating position of separate SC+R+S) = 1. None, no veins distinguishable = 2. NONADDITIVE (C50)
101. Closed cells in hindwing (sixth variable): One or more (or none but unlike States 1 and 2) = 0. None, vein C short but distinct and vein SC+R+S long (veins running along and some distance from margin, latter continuous with crease in membrane indicating po-

- sition of SC+R+S) = 1. None, vein C absent except at extreme base and vein SC+R+S short (vein running some distance from margin and continuous with longitudinal crease in membrane indicating position of SC+R+S) = 2. (C50)
- [Variables 98-101: modification of V86 and addition of variables for conditions in Chrysidoidea and *Olixon*; Carpenter (1986, considering nebulous veins also) corrected.]
102. Hindwing empusal, anal and jugal veins: All three present = 0. Empusal well-developed, anal present, jugal absent = 1. Empusal well-developed, anal and jugal absent = 2. Empusal minute, anal and jugal absent = 3. [Reformulation of C51 and addition of state for conditions in various Chrysidoidea; Brothers (1975) and Carpenter (1986) corrected.]
103. Hindwing cross-vein cu-e: Originating basal to separation of veins M and Cu = 0. Originating distal to separation of veins M and Cu = 1. (C52, V89)
104. Hindwing vein Cu: Distinct distal to separation from vein M = 0. Obliterated distal to separation from vein M = 1. (C53, V90)
105. Basal hamuli (first variable): Dispersed along costal margin (or absent) = 0. Concentrated into a basal cluster = 1. (C54, V91)
106. Basal hamuli (second variable): Present = 0. Absent = 1. (C54, V92)
107. Plical lobe: Indicated by moderate incision = 0. Indicated by shallow notch = 1. Not indicated on margin = 2. (C55, V93)
108. Jugal lobe (first variable): Long and indicated by a notch (or absent) = 0. Moderately long and indicated by incision extending about half length of lobe = 1. Small and indicated by incision extending almost to base of wing = 2. (C56, V94)
109. Jugal lobe (second variable): Present = 0. Absent = 1. (C56, V95)
110. Leg form of female (first variable): All similar, slender and generalized (or modified differently from State 1) = 0. Mid- and hindlegs stout with femora and tibiae expanded; foreleg and all tarsi fairly slender = 1.
111. Leg form of female (second variable): All similar, slender and generalized (or modified differently from State 1) = 0. All femora inflated and fusiform although midfemur often less so; tibiae and tarsi fairly slender = 1. Profemur greatly swollen and protibia much expanded; other femora inflated and fusiform; tibiae and tarsi fairly slender = 2.
112. Leg form of female (third variable): All similar, slender and generalized (or modified differently from State 1) = 0. Profemur swollen; other femora and all tibiae slender; all tarsi flattened and expanded = 1.
- [Variables 110-112: limitation of C57 to female for clarity and elaboration for conditions in some Chrysidoidea.]
113. Arolium (first variable): Well-developed = 0. Not distinguishable = 1. (C58, V99)
114. Arolium (second variable): Similar on all legs = 0. Much enlarged on foreleg only = 1. [Variable added for condition in Sclerogibbidae.]
115. Claws: Ventrally toothed or cleft = 0. Ventrally simple = 1. (C59, V100)
116. Protibial calcar (first variable): Approximately straight and parallel-sided or triangular with an elongate inner lamina or pectination (or inwardly curved and hollowed along posterior surface) = 0. Strongly inwardly curved, not hollowed along posterior surface and more or less even in width with a small outer spine at apex = 1. Strongly inwardly curved, not hollowed along posterior surface and more or less even in width with apex obtuse = 2. (C60, V101)
117. Protibial calcar (second variable): Approximately straight and parallel-sided or triangular with an elongate inner lamina or pectination (or strongly inwardly curved and not hollowed along posterior surface) = 0. Inwardly curved, hollowed along posterior surface and with apex acute = 1. Inwardly curved, hollowed along posterior surface and with apex obtuse = 2. (C60)
- [Variables 116-117: reformulation for clarity and addition of intermediate state in V102 for condition in Proscoliinae.]

118. Mesotibial spines (first variable): Many scattered spiniform setae (or neither spines nor spiniform setae) = 0. Scattered weak (or very strong) spines = 1. Scattered moderately strong spines = 2. Spines moderate and present only apically = 3. Spines very strong and present only apically = 4. (C61, V103)
119. Mesotibial spines (second variable): Spines weak or absent (or strong but present only apically) = 0. Scattered very strong spines = 1. (C61, V104)
120. Mesotibial spines (third variable): Spiniform setae or spines present = 0. Neither spines nor spiniform setae but some slender setae much elongated = 1. (C61, V105)
121. Metatibial spines (first variable): Many scattered spiniform setae (or neither spines nor spiniform setae) = 0. Scattered weak (or very strong) spines = 1. Scattered moderately strong spines = 2. Spines moderate and present only apically = 3. Spines very strong and present only apically = 4. (C62, V106)
122. Metatibial spines (second variable): Spines weak or absent (or strong but present only apically) = 0. Scattered very strong spines = 1. (C62, V107)
123. Metatibial spines (third variable): Spiniform setae or spines present = 0. Neither spines nor spiniform setae but some slender setae much elongated = 1. (C62, V108)
124. Mesotibial spur number (first variable): Two (or none) = 0. One = 1. (C63, V109)
125. Mesotibial spur number (second variable): Two (or one) = 0. None = 1. (C63, V110)
126. Basic form of meso- and metatibial spurs (first variable): Simple, narrowly conical and circular in cross-section = 0. Slightly flattened dorsally with margins simple (or dorsally flattened with margins dentate or simple) = 1. Dorsally flattened with margins serrate = 2. (C64, V111)
127. Basic form of meso- and metatibial spurs (second variable): Simple, narrowly conical and circular in cross-section (or modified differently from States 1 and 2) = 0. Dorsally flattened with margins deeply dentate = 1. Dorsally flattened and elongate with few or no teeth on margins = 2. [States 2 and 3, *Bradynobaeninae* male and female respectively, combined.] (C64, V112)
128. Mesotibial calcar (first variable): Spurs similar and neither modified as calcar (or calcar formed by dorsal pectination only) = 0. Inner spur modified as calcar by dorsal pectinate carina = 1. (C65, V113)
129. Mesotibial calcar (second variable): Spurs similar and neither modified as calcar (or calcar formed by dorsal pectinate carina) = 0. Spur modified as calcar by dorsal pectination only = 1. (C65, V114)
130. Form of metacoxa: Smoothly rounded dorsally = 0. With dorsal longitudinal carina = 1. With dorsal longitudinal lamella = 2. (C66, V115)
131. Metatibial spur number: Two = 0. One = 1. (C67, V116)
132. Metatibial calcar (first variable): Spurs similar and neither modified as calcar (or modified differently from States 1 and 2) = 0. Inner spur modified as calcar by formation of dorsal tuft of bristles with little modification of cuticular portion = 1. Inner spur modified as calcar by formation of dorsal tuft of bristles and development of finely pectinate dorsal carina = 2. (C68)
133. Metatibial calcar (second variable): Spurs similar and neither modified as calcar (or modified differently from States 1 and 2) = 0. Inner spur modified as calcar by dorsal carinate expansion of cuticle over a considerable length = 1. Inner spur modified as calcar by dorsal carinate expansion of cuticle over less than half its length = 2. NONADDITIVE (C68)
[Variables 132-133: addition of states to V117 and V118 for conditions in *Olixon* and *Heterogynaidae*.]
134. Metatibial calcar (third variable): Spurs similar and neither modified as calcar (or modified differently from State 1) = 0. Inner spur modified as calcar by pectinate elaboration of dorsal carina = 1. (C68, V119)
135. Metatibial calcar (fourth variable): Spurs similar and neither modified as calcar (or modified differently from State 1) = 0. Inner

- spur modified as calcar by dorsal pectination without carina = 1. (C68, V120)
136. Metatibial calcar (fifth variable): Spurs similar and neither modified as calcar (or modified differently from State 1) = 0. Inner spur modified as calcar with dorsal blunt longitudinal setose carina = 1. [Variable added for condition in some Chrysidoidea.]
137. Mesosoma of apterous or micropterous female (first variable): Similar to that of male or macropterous female (or modified differently from States 1, 2 and 3) = 0. Proportions different from those of male or macropterous female, with pro-meso- and meso-metathoracic articulations functional, mesonotal subdivisions distinguishable but scutum reduced, metapostnotum very short, propleura free and not swollen, prepectal sclerite small and free, mesepimeron distinct and metepimeron well-developed = 1. As for State 1 but mesepimeron not distinguishable externally = 2. As for State 2 but mesonotal subdivisions not distinguishable and prepectal sclerite reduced = 3. (C69, V121)
138. Mesosoma of apterous or micropterous female (second variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. As for Variable 137 State 1 but mesepimeron not distinguishable externally and metepimeron much reduced and visible only at dorsal extremity = 1. (C69)
139. Mesosoma of apterous or micropterous female (third variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with pleura flattened, meso-metathoracic suture obliterated dorsally and prepectus fused with mesepisternum = 1. As for State 1 but promesothoracic articulation functional and metathoracic-propodeal suture obliterated dorsally = 2. (C69, V122)
140. Mesosoma of apterous or micropterous female (fourth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. As for Variable 139 State 1 but pro-mesothoracic articulation distinct although not functional and metathoracic-propodeal suture indistinct dorsally = 1. (C69, V123)
141. Mesosoma of apterous or micropterous female (fifth variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with mesopleuron somewhat protuberant, promesothoracic articulation functional, meso-metathoracic suture visible but not functional, mesonotum neither reduced nor enlarged and fused with mesepisternum = 1. As for State 1 but mesonotum very short and transverse = 2. (C69, V124)
142. Mesosoma of apterous or micropterous female (sixth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. As for Variable 141 State 1 but mesopleuron protuberant, meso-metathoracic suture indistinct and mesonotum somewhat posteriorly produced = 1. (C69, V125)
143. Mesosoma of apterous or micropterous female (seventh variable): Similar to that of male or macropterous female (or modified differently from States 1 and 2) = 0. Proportions different from those of male, with propleura fused to form a rigid tube and with deep lateral and ventral constriction between meso- and metathorax = 1. Proportions different from those of male, with most mesosomal sutures and subdivisions distinct and metapostnotum much enlarged = 2. NONADDITIVE (C69)
144. Mesosoma of apterous or micropterous female (eighth variable): Similar to that of male or macropterous female (or modified differently from State 1) = 0. Proportions different from those of male, with pronotum much enlarged, pro-meso- and meso-metathoracic articulations functional and propleura free and greatly swollen = 1. Proportions different from those of male and macropterous female, with pronotum enlarged, pro-mesothoracic articulation functional, mesonotal subdivisions distinguishable, meso-metathoracic pleural suture fused

and prepectus fused with pronotum = 2. Proportions different from those of male and macropterous female, with pro-mesonotal suture functional, meso-metanotal and metanotal propodeal sutures indistinct, meso-metapleural suture distinct and metapleural-propodeal suture indistinct = 3. NONADDITIVE

- [Variables 137-144: reformulation to refer to the adaptive complex of the mesosoma only when apterous or micropterous rather than being confounded by simultaneous consideration of independent mechanisms governing degree of wing development; addition of states and variable for conditions in *Olixon*, *Diamminae*, *Heterogynaidae*, *Sclerogibbidae*, *Embolemyidae* and *Formicidae*.]
145. 'Felt lines' (first variable): Absent (or modified differently from State 1) = 0. Lateral longitudinal pubescent depression on metasomal tergum II and sternum II = 1. (C70, V127)
 146. 'Felt lines' (second variable): Absent (or modified differently from States 1 and 2) = 0. Pubescent felt line on metasomal tergum II only = 1. Longitudinal cuticular invagination on metasomal tergum II = 2. (C70, V128)
 147. Stridulitra (first variable): Absent (or paired) = 0. Single narrow stridulitrum basally on metasomal tergum III = 1. Single very broad stridulitrum basally on metasomal tergum III = 2. NONADDITIVE (C71) [State added to V129 for condition in *Olixon*.]
 148. Stridulitra (second variable): Absent (or one) = 0. Pair of stridulitra basally on metasomal tergum IV = 1. (C71, V130)
 149. Junction of metasomal terga I and II: Smoothly continuous = 0. Slightly constricted = 1. Strongly constricted and first segment nodose = 2. (C72, V131)
 150. Metasomal petiole: None, segment evenly narrowed anteriorly = 0. Distinct, segment cylindrical anteriorly = 1. (C73, V132)
 151. Lateral margin of metasomal tergum I (first variable): Entirely broadly overlying sternum I and articulating with it anteriorly (or very broadly overlying sternum I posteriorly but fused with it anteriorly) = 0. Narrowly overlying sternum I posteriorly, abutting it and not movable anteriorly = 1. Narrowly overlying sternum I posteriorly and fused with it along petiole = 2. (C74, V133)
 152. Lateral margin of metasomal tergum I (second variable): Entirely broadly overlying sternum I and articulating with it anteriorly (or narrowly overlying sternum I posteriorly) = 0. Very broadly overlying sternum I posteriorly but strongly narrowed and fused with laterodorsal face of sternum I anteriorly = 1. [Variable added for condition in *Chrysidoidea*.]
 153. Width of metasomal tergum I: Entirely about as wide as or broader than sternum I = 0. Much narrower than sternum I anteriorly = 1. Absent anteriorly, petiole entirely formed by sternum I = 2. (C75, V134)
 154. Differentiation of metasomal sternum I: Thin and overlying or abutting sternum II without any marked discontinuity = 0. Depressed posteriorly and differentiated from sternum II by a marked constriction = 1. Thick and abutting sternum II = 2. Forming posterior lobules = 3. Thick and overlapping sternum II = 4. NONADDITIVE (C76) [States added to V135 for conditions in various *Chrysidoidea*, see Rasnitsyn (1980) and Carpenter (1986), and for *Fedtschenkiinae*.]
 155. Junction of metasomal terga II and III: Smoothly continuous = 0. Strongly constricted = 1. (C77, V136)
 156. Reduction of metasomal terga of female (first variable): Tergum VII partly exposed and evenly sclerotized (or modified differently from States 1 and 2) = 0. Tergum VI exposed and evenly sclerotized, tergum VII hidden and considerably desclerotized with an anterior short sclerotized strip connecting lateral spiracular plates = 1. Tergum VI exposed and evenly sclerotized, tergum VII hidden and very considerably desclerotized with lateral spiracular plates unconnected by any sclerotized strip = 2. (C78, V137)
 157. Reduction of metasomal terga of female (second variable): Six or seven terga exposed and evenly sclerotized = 0. Four terga ex-

- posed and evenly sclerotized, terga V to VII hidden and desclerotized = 1.
158. Reduction of metasomal terga of female (third variable): Tergum VII exposed and evenly sclerotized (or modified differently from State 1) = 0. Tergum VII hidden under enlarged sternum VI and scarcely desclerotized = 1.
159. Reduction of metasomal terga of female (fourth variable): Tergum VII exposed and evenly sclerotized (or modified differently from State 1) = 0. Tergum VII hidden under tergum VI but scarcely desclerotized = 1.
[Variables 157-159: variables added to C78 for conditions in various Chrysidoidea.]
160. Articulation within gonocoxite IX of female: Absent = 0. Present = 1. (C79, V138)
161. Valve comprising paired valvilli on gonapophysis VIII of female: Present = 0. Absent = 1. (C80, V139) [See Quicke, Fitton & Ingram (1992) for further justification of polarity.]
162. Gonapophysis IX of female (first variable): Weakly arcuate dorsally (or almost straight) = 0. Strongly arcuate dorsally with apex directed downward = 1. (C81, V140)
163. Gonapophysis IX of female (second variable): Weakly (or strongly) arcuate dorsally with apex directed obliquely (or strongly) ventrally = 0. Almost straight or slightly arcuate ventrally with apex directed posteriorly or slightly upward = 1. (C81, V141)
164. Metasomal sternum VII of male: Well-developed and exposed = 0. Reduced and partly exposed = 1. Much reduced and concealed = 2. (C82, V142)
165. Form of male hypopygium (first variable): Simple (or apically lobed or spined) = 0. Peglike and not acute apically = 1. (C83, V143)
166. Form of male hypopygium (second variable): Simple (or modified differently from States 1 and 2) = 0. Elongate with apex trilobed = 1. Elongate with three subequal apical spines about as long as base excluding anterior processes = 2. (C83) [Intermediate state added to V144 for condition in Proscoliinae.]
167. Form of male hypopygium (third variable): Simple (or modified differently from State 1) = 0. Apically forming a single long upcurved spine = 1. (C83, V145)
168. Form of male hypopygium (fourth variable): Simple (or modified differently from States 1 and 2) = 0. Apically trispinose with middle spine upcurved and much longer than laterals which much shorter than base of hypopygium = 1. Apically trispinose with middle spine straight and slightly longer than laterals which much shorter than base of hypopygium = 2. (C83, V146)
169. Concealment of male hypopygium (first variable): Exposed (or more than basal half concealed) = 0. Up to basal half concealed = 1. (C84, V147)
170. Concealment of male hypopygium (second variable): Exposed (or no more than half concealed) = 0. Almost or completely concealed = 1. (C84, V148)
171. Cercus of male: Present = 0. Absent = 1. (C85, V149)
172. Gonapophyses IX of male (first variable): Fused dorsally over much of length (or modified differently from State 1) = 0. Linked dorsally by membrane over most of length = 1. (C86, V150)
173. Gonapophyses IX of male (second variable): Fused dorsally over much of length (or modified differently from State 1) = 0. Free over most of length and linked only basally by membrane = 1. (C86, V151)
174. Gonapophyses IX of male (third variable): Simple and fused dorsally over much of length (or modified differently from State 1) = 0. Forming basal bulge and apical lobe and fused dorsally over most of length = 1. [Variable added to C86 for condition in Thynninae, see Kimsey (1991).]
175. Larval mandibular teeth (first variable): Four (two or one) = 0. Three = 1. (C87, V152)
176. Larval mandibular teeth (second variable): Four (three or one) = 0. Two = 1. (C87, V153)
177. Larval mandibular teeth (third variable): Four (three or two) = 0. One = 1. (C87, V154)

178. Larval spiracles: Ten pairs fully developed, of similar size and complexity = 0. Nine pairs fully developed, second thoracic pair much reduced although still distinguishable = 1. Nine pairs fully developed, first thoracic pair apparently absent = 2. NONADDITIVE (C88) [State added to V155 for condition in Typhoctini (unpublished data).]
179. Number of prey: One = 0. Many = 1. (C89, V156)
180. Nesting (first variable): Prey not relocated, no nest construction (or host cavity closed) = 0. Prey relocated, no nest construction (or nest constructed but not closed, or pre-existing cavity closed off) = 1. Prey relocated, nest constructed and closed = 2. (C90, V157)
181. Nesting (second variable): Prey not relocated, no nest construction (or modified differently from State 1) = 0. Prey relocated, nest constructed but not closed = 1. (C90, V158)
182. Nesting (third variable): Prey not relocated, no nest construction (or modified differently from State 1) = 0. Prey relocated into pre-existing cavity which closed = 1. (C90, V159)
183. Nesting (fourth variable): Prey not relocated and no nest construction (or prey relocated) = 0. Prey not relocated and host cavity closed = 1. (C90, V160)
184. Oviposition sequence: On prey or host = 0. In empty cell before prey location = 1. (C91, V161)
185. Type of provisions: Arthropods = 0. Plant matter = 1. (C92, V162)
186. Third mesosomal phragma of macropterous form (first variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from States 1, 2 or 3) = 0. Forming even narrow flange with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 1. Absent medially with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 2. Entirely absent with muscles *2ph-3ph* attaching on widely separated areas of metapostnotum = 3.
187. Third mesosomal phragma of macropterous form (second variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from States 1, 2 and 3) = 0. Forming distinct even flange laterally or entirely with muscles *2ph-3ph* large and attaching over medial area of variously developed metapostnotum and phragma = 1. Medially reduced (or expanded as a thin plate, or expanded laterally) with muscles *2ph-3ph* attaching on adjacent (or separated) areas on either side of midline of metapostnotum and/or phragma = 2. Much reduced over most of width with muscles *2ph-3ph* lost = 3.
188. Third mesosomal phragma of macropterous form (third variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Expanded medially as a thin plate with muscles *2ph-3ph* attaching on narrow adjacent areas on either side of midline of phragma = 1.
189. Third mesosomal phragma of macropterous form (fourth variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Absent with muscles *2ph-3ph* much reduced and attaching at small separated points = 1.
190. Third mesosomal phragma of macropterous form (fifth variable): Forming distinct even flange with muscles *2ph-3ph* attaching on narrowly separated areas of metapostnotum and phragma (or modified differently from State 1) = 0. Weakly expanded laterally with muscles *2ph-3ph* small and attaching on somewhat separated areas of phragma = 1. Strongly expanded laterally with muscles *2ph-3ph* small basally and attaching on broadly separated areas of phragma = 2. Strongly expanded laterally as plates with muscles *2ph-3ph* very large and attaching on

broadly separated areas of phragma = 3.
NONADDITIVE

191. Second mesosomal phragma of macropterous form (first variable): Strongly oblique with dorsal posterior extremity of muscles *1ph-2ph* far anterior to ventral extremity and muscles *2ph-3ph* attaching on its anterior half (or modified differently from State 1) = 0. Scarcely oblique posteriorly with dorsal posterior extremity of muscles *1ph-2ph* only slightly anterior to ventral extremity and muscles *2ph-3ph* attaching on its anterior half = 1.
192. Second mesosomal phragma of macropterous form (second variable): Strongly (or scarcely) oblique posteriorly with muscles *2ph-3ph* attaching on its anterior half = 0. Scarcely oblique posteriorly with dorsal posterior extremity of muscles *1ph-2ph* only slightly anterior to ventral extremity and muscles *2ph-3ph* attaching on its posterior half = 1.
[Variables 186-192: new characters modified and extended from Brothers (1976), polarized by reference to non-*aculeates*, newly scored.]
193. Mesocoxal subdivision and insertion: Mesocoxa subdivided by a broad sulcus into large basicoxite and disticoxite and mesocoxal cavities large and approximated or narrowly separated medially = 0. Mesocoxa subdivided by a broad sulcus into large basicoxite and disticoxite and mesocoxal cavities large and widely separated = 1. Mesocoxa subdivided by a fairly deep sulcus into reduced basicoxite and large disticoxite and mesocoxal cavities moderate and widely separated = 2. Mesocoxa subdivided by a deep narrow sulcus into much-reduced basicoxite and large disticoxite and mesocoxal cavities small and widely separated = 3. [New character from Johnson (1988), modified and checked.]
194. Hypopharynx pubescence: Present = 0. Reduced = 1. [New character from Rasnitsyn (1980, 1988), not checked.]
195. Metasomal sternum I and tergum II: Not articulated, tergum II not touching or freely overlying or underlying lateral extremities of sternum I = 0. Articulated, tergum II overlying lateral extremities of sternum I = 1. Hinged, tergum II underlying lateral extremities of tergum I = 2. [New character modified from Rasnitsyn (1980, 1988), rescored.]
196. Mesotrochantellus: Distinctly present = 0. Reduced but discernible = 1. Absent = 2. [New character from Rasnitsyn (1980, 1988) with state added to describe variation more accurately, rescored.]
197. Mandibles: 'Chewing type' = 0. 'Cutting type' = 1. [New character from Rasnitsyn (1980, 1988), rescored.]
198. Female cerci: Present = 0. Absent = 1. [New character from Rasnitsyn (1980, 1988), scored as by Rasnitsyn (1980, not 1988) and checked.]
199. Metasomal sternum VI of female (first variable): Convex apically with lateral areas not strongly differentiated nor produced; sting aperture formed by sternum VI and tergum VI or VII = 0. Convex apically with lateral areas strongly differentiated and dorsomesally produced; sting aperture formed by sternum VI and narrow = 1. Depressed apically with lateral areas very strongly differentiated and dorsomesally produced; sting aperture formed by sternum VI and broadly slitlike = 2.
200. Metasomal sternum VI of female (second variable): With lateral areas not strongly differentiated and sting aperture formed by sternum VI and tergum VI or VII (or lateral areas strongly differentiated) = 0. With lateral areas not differentiated but dorsomesally produced; sting aperture formed by sternum VI and circular = 1.
[Variables 199-200: new character re-evaluated and modified from Rasnitsyn (1980, 1988), rescored.]
201. Forewing vein S2: Present = 0. Absent = 1. [Polarized as by Carpenter (1986).]
202. Free furcula in female ovipositor: Present, gonapophysis IX without acute anterodorsal process = 0. Absent, probably fused with gonapophysis IX as acute anterodorsal pro-

- cess = 1. [Polarized as by Oeser (1961), Carpenter (1986).]
203. Articulation between gonocoxite IX and gonapophysis IX in female: Present = 0. Absent = 1.
204. Larval arthropod food source: Coleoptera larva = 0. Embioptera = 1. Auchenorrhyncha = 2. Tenthredinoidea cocoon or Phasmida egg = 3. Gryllotalpidae only = 4. Aculeata larva or pupa = 5. Araneae = 6. Gryllidae only = 7. Blattodea and/or Orthoptera = 8. Solifugae = 9. NONADDITIVE
205. Larval lifestyle: Freelifving, predatory or ectoparasitic without cyst formation = 0. Endoparasitic initially with external cyst formation after first instar = 1. Entirely ectoparasitic with cyst formation after first instar = 2. NONADDITIVE
206. Anterior pedicels of tentorium: Broad = 0. Rodlike = 1. Rodlike with lamellar processes = 2.
207. Prothoracic furca: Vertical = 1. Proclined = 1. Proclined and 'modified' = 2.
208. Metasomal sternum II anterior margin: Transversely curved = 0. Transversely straight with lateral notches = 1. With expanded lateral desclerotized areas = 2. With median notch = 3. NONADDITIVE
209. Head form (first variable): Not of prognathous 'bethylid type' = 0. Of 'bethylid type' (more or less prognathous with genal and postgenal bridges enlarged and eyes often reduced) = 1.
210. Head form (second variable): Not concave posteriorly and without sharp carina on vertex and gena = 0. Concave posteriorly with sharp carina on vertex and gena = 1.
[Variables 201-210: new characters from Carpenter (1986) and Rasnitsyn (1980, 1988); Variable 204 including unpublished information; Variable 205 including information from Gurney (1953); Variables 206-208 not checked; Variable 210 by DJB, polarized by reference to non-aculeates.]
211. Clypeal form: Without any median longitudinal carina = 0. With median longitudinal carina = 1.
212. Antennal prominence: Absent = 0. Present = 1.
213. Pedicel-flagellum articulation: Movable = 0. Fixed = 1.
[Variables 211-213: new characters from Carpenter (1986) and Rasnitsyn (1980, 1988), checked.]
214. Metacoxal cavities: Open, without any posterolateral projection of metasternum = 0. Open but with metasternum posteriorly produced on each side to narrow opening posteromesally = 1. Closed = 2. [New character from Kimsey (1991), extended and modified, rescored.]
215. Forewing vein Cu2: Present, reaching vein E = 0. Much reduced or absent, not reaching vein E = 1.
216. Larval galea: Well-developed = 0. Much reduced = 1. Absent = 2.
217. Larval head parietal bands: Absent or very weak = 0. Strong = 1.
218. Larval antenna: With 3 sensilla = 0. With 2 sensilla = 1. With 4 to 6 sensilla = 2. NONADDITIVE
219. Larval spinneret: A median transverse slit = 0. Paired spigots = 1.
[Variables 215-219: new characters by DJB, polarized by reference to non-aculeates.]

APPENDIX VII

Distribution of derived character states on preferred cladogram (see text) of 34 taxa of Aculeata (Fig. 9b) resulting from analysis of data in Table IV; optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 201 and 216. Unnamed internodes are referred to by listing the subtended terminal superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'.

Final weights of variables (10 is maximum):
Weight = 10: 3, 8, 9, 17, 18, 19, 20, 25, 28, 31, 32, 35, 36, 39, 42, 45, 47, 49, 51, 52, 53, 59, 60, 64, 65, 69, 72, 74, 76, 78, 79, 87, 88, 89, 90, 91, 92, 97, 98, 99, 100, 101, 103, 108, 111, 112, 114, 116, 117, 119, 120, 122, 123,

125, 127, 128, 129, 131, 134, 135, 136, 137, 138, 139, 140, 141, 142, 143, 144, 146, 147, 150, 151, 152, 153, 155, 157, 158, 159, 160, 165, 166, 167, 168, 172, 173, 174, 181, 182, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 210, 211, 212, 213, 215, 219

Weight = 6: 85

Weight = 5: 48, 156, 178, 216

Weight = 4: 57, 75, 149, 154, 187

Weight = 3: 15, 23, 34, 70, 73, 86, 132, 196

Weight = 2: 4, 6, 16, 22, 29, 40, 44, 55, 62, 63, 77, 104, 105, 113, 118, 121, 148, 175, 183, 194, 195, 197, 199, 208, 217

Weight = 1: 7, 11, 13, 21, 30, 38, 46, 54, 56, 58, 61, 71, 84, 93, 94, 102, 106, 107, 109, 110, 126, 130, 163, 180, 188

Weight = 0: 1, 2, 5, 10, 12, 14, 24, 26, 27, 33, 37, 41, 43, 50, 66, 67, 68, 80, 81, 82, 83, 95, 96, 115, 124, 133, 145, 161, 162, 164, 169, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): 43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1, 164:0>1, 193:0>1, 197:0>1, 198:0>1

(Chrysidoidea): 33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1, 186:0>1, 193:1>3, 196:0>1, 207:0>1, 215:0>1

Plumariidae: 2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2

(Scolebythidae, Bethyliidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethyliidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1

(Bethyliidae, Chrysididae): 13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2

Bethyliidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>1

(Sclerogibbidae, Dryinidae, Embolemidae): 11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1

Sclerogibbidae: 2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2

(Dryinidae, Embolemidae): 20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2

Drynidae: 30:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): 18:0>1, 37:0>1, 44:0>1, 66:0>1, 96:0>1, 156:0>1, 187:0>1, 201:0>1

(Apoidea): 35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1, 126:0>2>, 163:0>1, 180:0>1, 192:0>1

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 124:0>1, 156:1>2, 164:1>2, 170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 193:1>0, 196:0>2, 208:0>3

(sphecids, Heterogynidae): 118:1>2, 121:1>2, 164:1>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, 193:1>0, 200:0>1, 204:0>8

Heterogynidae: 2:0>1, 37:1>0, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 126:2>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1, 193:1>2,

(Vespoidea): 13:0>1, 40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1

Sierolomorphidae: 68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, 130:0>1, 164:1>0, 165:0>1, 170:0>1, 190:0>1, 193:1>2, 200:0>1

(Rhopalosomatidae, Vespidae, Scoliidae, Formicidae, Bradynobaenidae, Pompilidae, Mutillidae, Sapygidae, Tiphiidae): 63:0>1, 80:1>0, 84:1>0, 108:0>1

(Rhopalosomatidae, Vespidae, Scoliidae, Formicidae, Bradynobaenidae): 30:0>1, 38:0>1, 46:0>1, 48:1>2, 93:0>1, 94:0>2, 105:0>1, 149:0>1, 163:0>1, 195:0>1

(Rhopalosomatidae): 56:1>2, 58:0>1, 92:0>1, 95:0>1, 112:0>1, 132:0>1, 194:1>0, 200:0>1, 204:0>7, 205:0>2

rhopalosomatids: 10:0>1, 63:1>0, 68:0>2, 70:0>1, 107:1>0, 177:0>1, 190:0>2, 219:0>1

- Olixon:** 33:0>1, 37:1>0, 38:1>0, 50:0>1, 55:0>1, 61:0>1, 80:0>2, 81:0>1, 83:0>1, 92:1>2, 93:1>2, 100:0>2, 118:1>0, 121:1>0, 132:1>2, 147:0>2, 210:0>1
- (Vespididae, Scoliidae, Formicidae, Bradynobaenidae): 34:0>1, 57:0>1, 61:0>1, 63:1>2, 154:0>1, 175:0>1, 180:0>1
- (Vespididae, Scoliidae): 5:0>1, 10:0>1, 13:1>0, 24:0>1, 34:1>2, 38:1>2, 43:1>2, 96:1>0, 106:0>1, 115:0>1, 163:1>0, 171:0>1, 180:1>2, 190:0>3, 217:0>1
- Vespididae:** 32:0>1, 34:2>3, 48:2>3, 56:1>0, 58:0>1, 82:0>1, 133:0>1, 149:1>0, 161:0>1, 179:0>1, 184:0>1, 193:1>0, 195:1>2
- (Scoliidae): 15:0>1, 31:0>1, 49:0>1, 54:0>1, 59:0>1, 73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1, 164:1>0, 166:0>1, 172:0>1, 199:1>2
- Scoliinae:** 67:0>1, 69:0>1, 77:0>1, 117:1>2, 124:0>1, 166:1>2, 170:0>1, 218:0>2
- Proscoliinae:** 5:1>0, 10:1>0, 24:1>0, 27:0>1, 38:2>1, 43:2>1, 66:1>0, 80:0>1, 81:0>1, 89:0>2, 94:2>1, 154:1>0, 169:0>1, 195:1>0
- (Formicidae, Bradynobaenidae): 55:0>1, 56:1>0, 94:2>0, 118:1>2, 121:1>3, 150:0>1, 193:1>3, 214:0>1
- Formicidae:** 3:0>1, 38:1>2, 50:0>1, 61:1>2, 72:0>1, 85:0>1, 106:0>1, 118:2>3, 128:0>1, 134:0>1, 144:0>3, 164:1>0, 179:0>1, 181:0>1, 184:0>1, 187:2>3, 214:1>2
- (Bradynobaenidae): 2:0>1, 16:0>1, 30:1>0, 34:1>0, 46:1>0, 73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1, 95:0>1, 107:1>2, 141:0>1, 146:0>1, 148:0>1, 151:0>1, 161:0>1, 180:1>0, 199:0>1
- (Typhoctinae): 4:0>1, 37:1>0, 38:1>0, 66:1>0, 121:3>2, 130:0>1, 141:1>2
- Eotillini:** 71:0>1, 93:1>0, 107:2>0, 113:0>1, 118:2>1, 121:2>1
- Typhoctini:** 96:1>0, 109:0>1, 178:0>2, 188:0>1, 204:0>9
- (Chyphotinae, Apterogyninae, Bradynobaeninae): 6:0>1, 9:0>1, 12:0>1, 13:1>0, 21:0>1, 110:0>1, 142:0>1, 151:1>2, 153:0>1, 168:0>1, 195:1>2
- Chyphotinae:** 61:1>2, 66:1>0, 81:0>1, 93:1>0, 153:1>2, 169:0>1
- (Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 47:0>1, 62:0>1, 78:1>2, 84:1>2, 91:0>1, 93:1>2, 95:1>2, 96:1>0, 106:0>1, 113:0>1, 116:0>1, 118:2>3, 126:0>1, 127:0>1, 148:1>0, 171:0>1
- Apterogyninae:** 130:0>1, 149:1>2, 155:0>1, 161:1>0, 193:3>1
- Bradynobaeninae:** 7:0>1, 12:1>0, 26:0>1, 28:0>1, 29:0>1, 36:0>1, 47:1>2, 60:0>1, 82:0>1, 83:0>1, 91:1>2, 97:0>1, 115:0>1, 116:1>2, 118:3>4, 121:3>4, 125:0>1, 127:1>2, 146:1>2, 162:0>1, 163:1>0, 168:1>2, 187:2>3, 195:2>1
- (Pompilidae, Mutillidae, Sapygidae, Tiphidae): 13:1>0, 118:1>2, 121:1>2, 178:0>1, 199:0>1
- (Pompilidae, Mutillidae, Sapygidae): 51:0>1, 58:0>1, 214:0>1
- Pompilidae:** 61:0>1, 63:1>0, 68:0>1, 94:0>2, 105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1
- (Mutillidae, Sapygidae): 6:0>1, 21:0>1, 37:1>0, 108:1>2, 130:0>1, 162:0>1, 173:0>1, 204:0>5
- (Mutillidae): 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 183:0>1, 193:1>3, 195:0>1
- Myrmosinae:** 14:0>1, 104:0>1, 130:1>2, 139:1>2, 164:1>0, 170:0>1
- mutillids:** 30:0>1, 34:0>1, 54:0>1, 62:0>1, 73:1>2, 80:0>1, 84:0>1, 95:0>1, 140:0>1, 145:0>1, 214:1>2
- (Sapygidae): 23:0>1, 58:1>0, 104:0>1, 161:0>1, 214:1>0
- Fedtschenkinae:** 23:1>2, 80:0>1, 81:0>1, 126:0>1, 154:0>4, 162:1>0
- Sapyginae:** 10:2>1, 25:0>1, 66:1>0, 118:2>0, 121:2>0, 164:1>2, 171:0>1, 176:0>1, 178:1>0, 199:1>0, 200:0>1, 218:0>1
- (Tiphidae): 37:1>0, 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 110:0>1, 199:1>2
- Anthoboscinae:** 107:1>0, 169:0>1, 193:1>0
- (Diamminae, Thynninae, Myzininae, Methochinae, Tiphinae, Brachycistidinae): 2:0>1, 7:1>0>1, 74:0>1, 80:0>1, 130:0>1, 137:0>1, 154:0>1
- Diamminae: 138:0>1, 180:0>1, 204:0>4
- (Thynninae, Myzininae, Methochinae, Tiphinae, Brachycistidinae): 7:0>1, 162:0>1, 214:0>1
- Thynninae:** 156:1>2, 174:0>1
- (Myzininae, Methochinae, Tiphinae, Brachycistidinae): 1:0>1, 81:0>1, 102:1>2, 107:1>0, 130:1>0, 167:0>1, 188:0>1, 195:0>1, 214:1>2
- Myzininae:** 2:1>0, 63:1>2, 133:0>1, 145:0>1, 162:1>0, 164:1>0
- (Methochinae, Tiphinae, Brachycistidinae): 37:0>1, 71:1>0, 137:1>2
- Methochinae:** 11:0>1, 14:0>1, 56:2>1, 80:1>2, 89:0>1, 96:0>1, 110:1>0, 118:2>1, 121:2>1, 129:0>1, 131:0>1, 135:0>1, 164:1>0, 183:0>1, 193:1>3
- (Tiphinae, Brachycistidinae): 1:1>0, 7:1>0, 34:0>1, 61:0>1, 66:0>1, 83:0>1, 84:0>1, 95:0>1, 130:0>1, 149:0>1, 164:1>2, 170:0>1, 171:0>1
- Tiphinae:** 2:1>0, 63:1>2, 74:1>2, 90:0>1
- Brachycistidinae:** 12:0>1, 16:0>1, 48:1>2, 106:0>1, 115:0>1, 124:0>1, 137:2>3, 188:1>0

APPENDIX VIII

Distribution of derived character states on preferred cladogram (see text) of family ground plans of Aculeata (Fig.10b) resulting from analysis of data in Tables IV and V; optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 201 and 216. Unnamed internodes are referred to by listing the subtended superfamilies or families. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'. Placements which agree with those on Fig. 9b are indicated in boldface. Variables invariant between family ground plans and thus excluded from this analysis: 1, 7, 9, 14, 17, 25, 28, 36, 47, 60, 62, 69, 71, 74, 89, 91, 97, 113, 116, 125, 127, 129, 131, 135, 137, 138, 140, 142, 145, 148, 153, 155, 167, 168, 174, 188, 210

Final weights of variables (10 is maximum):

Weight = 10: 3, 4, 5, 8, 10, 12, 15, 18, 19, 20, 24, 26, 31, 32, 34, 35, 39, 42, 45, 49, 50, 51, 52, 53, 59, 64, 65, 67, 72, 76, 78, 79, 82, 87, 88, 90, 92, 98, 99, 100, 101, 103, 104, 106, 108, 111, 112, 114, 117, 119, 120, 122, 123, 128, 133, 134, 136, 139, 141, 143, 144, 146, 147, 151, 152, 156, 157, 158, 159, 160, 162, 165, 166, 169, 172, 173, 181, 182, 183, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 211, 212, 213, 215, 219

Weight = 6: 48, 85

Weight = 5: 187, 216

Weight = 4: 29, 85

Weight = 3: 38, 57, 63, 70, 77, 86, 107, 126, 149, 178, 196

Weight = 2: 6, 11, 40, 44, 80, 102, 105, 109, 118, 121, 154, 163, 175, 180, 194, 195, 197, 199, 208, 217

Weight = 1: 13, 21, 30, 37, 56, 61, 73, 81, 84, 93, 94, 115, 130

Weight = 0: 2, 16, 22, 23, 27, 33, 41, 43, 46, 54, 55, 58, 66, 68, 75, 83, 95, 96, 110, 124, 132, 150, 161, 164, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): 43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1, 193:0>2, 197:0>1, 198:0>1

(Chrysidoidea): 33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1, 164:0>1, 186:0>1, 193:2>3, 196:0>1, 207:0>1, 215:0>1

Plumariidae: 2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2

(Scolebythidae, Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1

(Bethylidae, Chrysididae): 13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2

Bethylidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>3

(Sclerogibbidae, Dryinidae, Embolemidae): 11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1

Sclerogibbidae: 2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2

(Dryinidae, Embolemidae): 20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2

Dryinidae: 30:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): 18:0>1, 44:0>1, 66:0>1, 96:0>1, 156:0>1, 187:0>1, 201:0>1

(Apoidea): 35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1, 118:1>2, 121:1>2, 126:0>1, 163:0>1, 192:0>1

Heterogynaidae: 2:0>1, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1

(sphecids, apids): 37:0>1, 126:1>2, 180:0>1, 193:2>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, 200:0>1, 204:0>8

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 118:2>1, 121:2>1, 124:0>1, 156:1>2, 164:0>2, 170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 196:0>2, 208:0>3

(Vespoidea): 40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1

Sierolomorphidae: 13:0>1, 37:0>1, 68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, 130:0>1, 165:0>1, 170:0>1, 190:0>1, 200:0>1

(Tiphidae, Pompilidae, Sapygidae, Mutillidae, Rhopalosomatidae, Bradynobaenidae, Formicidae, Scoliidae, Vespidae): 63:0>1, 80:1>0, 84:1>0, 108:0>1, 164:0>1

(Tiphidae, Pompilidae, Sapygidae, Mutillidae): 118:1>2, 121:1>2, 178:0>1, 193:2>1, 199:0>1

Tiphidae: 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 107:1>0, 110:0>1, 169:0>1, 193:1>0, 199:1>2

(Pompilidae, Sapygidae, Mutillidae): 51:0>1, 58:0>1, 214:0>1

Pompilidae: 37:0>1, 61:0>1, 63:1>0, 68:0>1, 94:0>2, 105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1

(Sapygidae, Mutillidae): 6:0>1, 21:0>1, 108:1>2, 130:0>1, 173:0>1, 204:0>5

Sapygidae: 23:0>1, 58:1>0, 66:1>0, 104:0>1, 118:2>1, 121:2>1, 161:0>1, 176:0>1, 178:1>0, 214:1>0, 218:0>1

Mutillidae: 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 162:0>1, 164:1>0, 183:0>1, 193:1>3, 195:0>1

(Rhopalosomatidae, Bradynobaenidae, Formicidae, Scoliidae, Vespidae): 30:0>1, 46:0>1, 48:1>2, 93:0>1, 105:0>1, 149:0>1, 163:0>1, 195:0>1

Rhopalosomatidae: 13:0>1, 56:1>2, 58:0>1, 63:1>0, 68:0>2, 70:0>1, 92:0>1, 94:0>1, 95:0>1, 107:1>0, 112:0>1, 132:0>1, 177:0>1, 190:0>2, 193:2>1, 194:1>0, 200:0>1, 204:0>7, 205:0>2, 219:0>1

(Bradynobaenidae, Formicidae, Scoliidae, Vespidae): 55:0>1, 56:1>0, 57:0>1, 61:0>1, 63:1>2, 96:1>0, 150:0>1, 154:0>1, 175:0>1, 214:0>1

Bradynobaenidae: 2:0>1, 16:0>1, 30:1>0, 46:1>0, 66:1>0, 73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1, 93:1>0, 95:0>1, 141:0>1, 146:0>1, 151:0>1, 178:0>2, 199:0>1, 204:0>9

(Formicidae, Scoliidae, Vespidae): 34:0>1, 37:0>1, 38:0>2, 106:0>1, 179:0>1, 180:0>1, 184:0>1

Formicidae: 3:0>1, 13:0>1, 50:0>1, 61:1>2, 72:0>1, 85:0>1, 96:0>1, 118:1>3, 121:1>3, 128:0>1,

134:0>1, 144:0>3, 164:1>0, 181:0>1, 187:2>3, 193:2>3, 214:1>2

(Scoliidae, Vespidae): 34:1>2, 55:1>0, 94:0>1, 115:0>1, 150:1>0, 163:1>0, 171:0>1, 180:1>2, 190:0>3, 193:2>1, 214:1>0, 217:0>1

Scoliidae: 15:0>1, 31:0>1, 38:2>1, 49:0>1, 54:0>1, 56:0>1, 59:0>1, 66:1>0, 73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1, 154:1>0, 164:1>0, 166:0>1, 172:0>1, 179:1>0, 184:1>0, 195:1>0, 199:0>2, 218:0>2

Vespidae: 5:0>1, 10:0>1, 24:0>1, 32:0>1, 34:2>3, 43:1>2, 48:2>3, 58:0>1, 82:0>1, 94:1>2, 133:0>1, 149:1>0, 161:0>1, 193:1>0, 195:1>2

APPENDIX IX

Distribution of derived character states on composite cladogram based on preferred results (see text) of all analyses of Aculeata (Fig. 11): optimization by accelerated transformation, except delayed transformation for variables considered unlikely to show reversals and manual for Variables 80, 95, 105, 109, 161, 201 and 216. Unnamed internodes are referred to by listing the subtended superfamilies, families or lower taxa. Character numbers refer to the variables in Appendix VI; transformations are denoted by listing the ancestral and derived states separated by a '>'. Placements which differ from those on Figs. 9b and/or 10b are in italics.

Weights of variables (10 is maximum):

Weight = 10: 1, 3, 8, 9, 17, 18, 19, 20, 25, 28, 31, 32, 35, 36, 39, 42, 45, 47, 49, 51, 52, 53, 59, 60, 64, 65, 69, 72, 74, 76, 78, 79, 87, 88, 89, 90, 91, 92, 97, 98, 99, 100, 101, 103, 108, 111, 112, 114, 116, 117, 119, 120, 122, 123, 125, 127, 128, 129, 131, 134, 135, 136, 138, 139, 140, 141, 142, 143, 144, 146, 147, 151, 152, 153, 155, 157, 158, 159, 160, 165, 166, 167, 168, 172, 173, 174, 181, 182, 185, 186, 189, 190, 191, 192, 198, 202, 203, 204, 205, 206, 207, 209, 210, 211, 212, 213, 215, 219

Weight = 6: 85, 137

Weight = 5: 48, 156, 178, 216

Weight = 4: 34, 57, 75, 149, 150, 154, 187

Weight = 3: 15, 23, 70, 73, 86, 132, 196

Weight = 2: 4, 6, 16, 22, 29, 38, 40, 44, 62, 63, 77, 104, 105, 106, 113, 121, 148, 175, 183, 194, 195, 197, 199, 208, 217

Weight = 1: 7, 11, 13, 21, 30, 46, 54, 55, 56, 58, 61, 84, 93, 94, 102, 107, 109, 110, 118, 126, 130, 163, 180, 188

Weight = 0: 2, 5, 10, 12, 14, 24, 26, 27, 33, 37, 41, 43, 50, 66, 67, 68, 71, 80, 81, 82, 83, 95, 96, 115, 124, 133, 145, 161, 162, 164, 169, 170, 171, 176, 177, 179, 184, 193, 200, 201, 214, 218

(Aculeata): 43:0>1, 80:0>1, 84:0>1, 102:0>2, 118:0>1, 121:0>1, 193:0>2, 197:0>1, 198:0>1

(Chrysidoidea): 33:0>1, 81:0>1, 85:0>1, 109:0>1, 111:0>1, 152:0>1, 160:0>1, 164:0>1, 186:0>1, 193:2>3, 196:0>1, 207:0>1, 215:0>1

Plumariidae: 2:0>1, 16:0>1, 29:0>1, 41:0>1, 143:0>1, 159:0>1, 161:0>1, 214:0>2

(Scolebythidae, Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 11:0>1, 13:0>1, 85:1>2, 95:0>1, 98:0>1, 118:1>0, 121:1>0, 186:1>2, 191:0>1, 197:1>0, 201:0>1, 206:0>1

Scolebythidae: 42:0>1, 43:1>0, 45:0>1, 95:1>2, 98:1>2, 120:0>1, 123:0>1, 164:1>0, 193:3>2

(Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae): 29:0>1, 33:1>0, 56:0>1, 64:0>1, 66:0>1, 136:0>1, 175:0>1, 186:2>3, 208:0>3, 216:0>1

(Bethylidae, Chrysididae): 13:1>0, 64:1>2, 80:1>2, 101:0>1, 154:0>3, 203:0>1, 208:3>2

Bethylidae: 6:0>1, 21:0>1, 22:0>1, 75:0>1, 83:0>1, 95:1>2, 101:1>2, 154:3>2, 164:1>0, 208:2>1, 209:0>1, 211:0>1, 216:1>2, 218:0>1

Chrysididae: 12:0>1, 27:0>1, 43:1>0, 48:0>1, 54:0>1, 56:1>0, 86:0>1, 157:0>1, 170:0>1, 171:0>1, 193:3>0, 204:0>3

(Sclerogibbidae, Dryinidae, Embolemidae): 11:1>0, 40:0>1, 44:0>1, 80:1>0, 93:0>1, 102:2>3, 177:0>1, 202:0>1, 214:0>1

Sclerogibbidae: 2:0>1, 8:0>1, 13:1>2, 19:0>1, 21:0>1, 33:0>1, 41:0>1, 53:0>1, 73:0>1, 81:1>2, 87:0>1, 95:1>2, 100:0>1, 111:1>2, 114:0>1, 144:0>1, 158:0>1, 161:0>1, 204:0>1, 207:1>2, 214:1>2

(Dryinidae, Embolemidae): 20:0>1, 38:0>1, 86:0>1, 99:0>1, 164:1>2, 170:0>1, 171:0>1, 196:1>2, 204:0>2, 205:0>1, 216:1>2

Dryinidae: 3:0>1, 40:1>0, 43:1>0, 44:1>0, 46:0>1, 56:1>0, 81:1>2, 86:1>2, 93:1>0, 124:0>1, 214:1>0, 218:0>1

Embolemidae: 26:0>1, 27:0>1, 32:0>2, 53:0>2, 57:0>2, 61:0>2, 66:1>2, 115:0>1, 144:0>2, 177:1>0, 197:0>1, 206:1>2, 208:3>1, 212:0>1, 213:0>1

(Aculeata s.s.): 18:0>1, 37:0>1, 44:0>1, 66:0>1, 96:0>1, 118:1>2, 121:1>2, 156:0>1, 187:0>1, 201:0>1

(Apoidea): 35:0>1, 39:0>1, 46:0>1, 52:0>1, 57:0>2, 61:0>1, 65:0>1, 70:0>1, 77:0>1, 93:0>1, 126:0>1, 163:0>1, 192:0>1

Heterogynaidae: 2:0>1, 37:1>0, 81:0>2, 90:0>2, 95:0>1, 109:0>1, 115:0>1, 130:0>1, 133:0>2, 143:0>2, 171:0>1, 187:1>0, 189:0>1

(sphecids, apids): 126:1>2, 180:0>1, 193:2>0

sphecids: 46:1>0, 84:1>0, 96:1>0, 102:2>0, 200:0>1, 204:0>8

apids: 4:0>1, 23:0>1, 39:1>2, 55:0>1, 67:0>1, 118:2>1, 121:2>1, 124:0>1, 156:1>2, 164:0>2, 170:0>1, 171:0>1, 176:0>1, 180:1>2, 185:0>1, 196:0>2, 208:0>3

(Vespoidea): 13:0>1, 40:0>1, 48:0>1, 56:0>1, 73:0>1, 107:0>1, 187:1>2, 194:0>1

Sierolomorphidae: 68:0>1, 81:0>1, 88:0>1, 95:0>1, 109:0>1, 118:2>1, 121:2>1, 130:0>1, 165:0>1, 170:0>1, 190:0>1, 200:3>1

(Rhopalosomatidae, Formicidae, Vespidae, Scoliidae, Bradynobaenidae, Pompilidae, Mutillidae, Sapygidae, Tiphiidae): 63:0>1, 80:1>0, 84:1>0, 108:0>1, 164:0>1

(Rhopalosomatidae, Formicidae, Vespidae, Scoliidae, Bradynobaenidae): 30:0>1, 38:0>1, 46:0>1, 48:1>2, 55:0>1, 93:0>1, 105:0>1, 149:0>1, 163:0>1, 195:0>1

(Rhopalosomatidae): 56:1>2, 58:0>1, 92:0>1, 94:0>2, 95:0>1, 112:0>1, 118:2>1, 121:2>1, 132:0>1, 193:2>1, 194:1>0, 200:0>1, 204:0>7, 205:0>2

rhopalosomatids: 10:0>1, 55:1>0, 63:1>0, 68:0>2, 70:0>1, 107:1>0, 177:0>1, 190:0>2, 219:0>1

Olixon: 33:0>1, 37:1>0, 38:1>0, 50:0>1, 61:0>1, 80:0>2, 81:0>1, 83:0>1, 92:1>2, 93:1>2, 100:0>2, 118:1>0, 121:1>0, 132:1>2, 147:0>2, 210:0>1

(Formicidae, Vespidae, Scoliidae, Bradynobaenidae): 56:1>0, 57:0>1, 61:0>1, 63:1>2, 150:0>1, 154:0>1, 175:0>1, 214:0>1

(Formicidae, Vespidae, Scoliidae): 34:0>1, 38:1>2, 106:0>1, 179:0>1, 180:0>1, 184:0>1

Formicidae: 3:0>1, 50:0>1, 61:1>2, 72:0>1, 85:0>1, 118:2>3, 121:2>3, 128:0>1, 134:0>1, 144:0>3, 164:1>0, 181:0>1, 187:2>3, 193:2>3, 214:1>2

(Vespidae, Scoliidae): 5:0>1, 10:0>1, 13:1>0, 24:0>1, 34:1>2, 43:1>2, 55:1>0, 94:0>2, 96:1>0, 115:0>1, 118:2>1, 121:2>1, 150:1>0, 163:1>0, 171:0>1, 180:1>2, 190:0>3, 193:2>1, 214:1>0, 217:0>1

- Vespidae:** 32:0>1, 34:2>3, 48:2>3, 58:0>1, 82:0>1, 133:0>1, 149:1>0, 161:0>1, 193:1>0, 195:1>2
- (Scoliidae): 15:0>1, 31:0>1, 49:0>1, 54:0>1, 56:0>1, 59:0>1, 73:1>0, 76:0>1, 79:0>1, 83:0>1, 84:0>1, 95:0>1, 107:1>2, 110:0>1, 117:0>1, 119:0>1, 122:0>1, 126:0>1, 164:1>0, 166:0>1, 172:0>1, 199:0>2
- Scoliinae:** 67:0>1, 69:0>1, 77:0>1, 117:1>2, 124:0>1, 166:1>2, 170:0>1, 179:1>0, 184:1>0, 218:0>2
- Proscoliinae:** 5:1>0, 10:1>0, 24:1>0, 27:0>1, 38:2>1, 43:2>1, 66:1>0, 80:0>1, 81:0>1, 89:0>2, 94:2>1, 154:1>0, 169:0>1, 195:1>0
- (Bradynobaenidae): 2:0>1, 16:0>1, 30:1>0, 46:1>0, 73:1>0, 75:0>1, 77:0>1, 78:0>1, 80:0>2, 84:0>1, 95:0>1, 107:1>2, 141:0>1, 146:0>1, 148:0>1, 151:0>1, 161:0>1, 193:2>3, 199:0>1,
- (Typhoctinae): 4:0>1, 37:1>0, 38:1>0, 66:1>0, 130:0>1, 141:1>2
- Eotillini:** 71:0>1, 93:1>0, 107:2>0, 113:0>1, 118:2>1, 121:2>1
- Typhoctini:** 96:1>0, 109:0>1, 178:0>2, 188:0>1, 204:0>9
- (Chyphotinae, Apterogyninae, Bradynobaeninae): 6:0>1, 9:0>1, 12:0>1, 13:1>0, 21:0>1, 110:0>1, 121:2>3, 142:0>1, 151:1>2, 153:0>1, 168:0>1, 195:1>2
- Chyphotinae:** 61:1>2, 66:1>0, 81:0>1, 93:1>0, 153:1>2, 169:0>1
- (Apterogyninae, Bradynobaeninae): 15:0>1, 17:0>1, 47:0>1, 62:0>1, 78:1>2, 84:1>2, 91:0>1, 93:1>2, 95:1>2, 96:1>0, 106:0>1, 113:0>1, 116:0>1, 118:2>3, 126:0>1, 127:0>1, 148:1>0, 171:0>1
- Apterogyninae:** 130:0>1, 149:1>2, 155:0>1, 161:1>0, 193:3>1
- Bradynobaeninae:** 7:0>1, 12:1>0, 26:0>1, 28:0>1, 29:0>1, 36:0>1, 47:1>2, 60:0>1, 82:0>1, 83:0>1, 91:1>2, 97:0>1, 115:0>1, 116:1>2, 118:3>4, 121:3>4, 125:0>1, 127:1>2, 146:1>2, 162:0>1, 163:1>0, 168:1>2, 187:2>3, 195:2>1
- (Pompilidae, Mutillidae, Sapygidae, Tiphidae): 13:1>0, 178:0>1, 193:2>1, 199:0>1
- (Pompilidae, Mutillidae, Sapygidae): 51:0>1, 58:0>1, 214:0>1
- Pompilidae:** 61:0>1, 63:1>0, 68:0>1, 94:0>2, 105:0>1, 126:0>1, 132:0>1, 161:0>1, 164:1>2, 175:0>1, 180:0>1, 182:0>1, 187:2>1, 194:1>0, 204:0>6, 217:0>1
- (Mutillidae, Sapygidae): 6:0>1, 21:0>1, 37:1>0, 108:1>2, 130:0>1, 162:0>1, 173:0>1, 204:0>5
- (Mutillidae): 2:0>1, 22:0>1, 51:1>2, 57:0>1, 81:0>2, 105:0>1, 139:0>1, 147:0>1, 154:0>1, 183:0>1, 193:1>3, 195:0>1
- Myrmosinae:** 14:0>1, 104:0>1, 130:1>2, 139:1>2, 164:1>0, 170:0>1
- mutillids:** 30:0>1, 34:0>1, 54:0>1, 62:0>1, 73:1>2, 80:0>1, 84:0>1, 95:0>1, 140:0>1, 145:0>1, 214:1>2
- (Sapygidae): 23:0>1, 58:1>0, 104:0>1, 161:0>1, 214:1>0
- Fedtschenkiinae:** 23:1>2, 80:0>1, 81:0>1, 126:0>1, 154:0>4, 162:1>0
- Sapyginae:** 10:0>1, 25:0>1, 66:1>0, 118:2>0, 121:2>0, 164:1>2, 171:0>1, 176:0>1, 178:1>0, 199:1>0, 200:0>1, 218:0>1
- (Tiphidae): 37:1>0, 56:1>2, 66:1>0, 96:1>0, 102:2>1, 103:0>1, 110:0>1, 199:1>2
- Anthoboscinae:** 107:1>0, 169:0>1, 193:1>0
- (Diamminae, Thynninae, Myzininae, Methochinae, Tiphinae, Brachycistidinae): 2:0>1, 71:0>1, 74:0>1, 80:0>1, 130:0>1, 137:0>1, 154:0>1
- Diamminae:** 138:0>1, 180:0>1, 204:0>4
- (Thynninae, Tiphinae, Brachycistidinae, Myzininae, Methochinae): 7:0>1, 162:0>1, 214:0>1
- Thynninae:** 156:1>2, 174:0>1
- (Tiphinae, Brachycistidinae, Myzininae, Methochinae): 37:0>1, 71:1>0, 81:0>1, 102:1>2, 107:1>0, 167:0>1, 188:0>1, 195:0>1, 214:1>2
- (Tiphinae, Brachycistidinae): 7:1>0, 34:0>1, 61:0>1, 66:0>1, 83:0>1, 84:0>1, 95:0>1, 149:0>1, 164:1>2, 170:0>1, 171:0>1
- Tiphinae:** 2:1>0, 63:1>2, 74:1>2, 90:0>1
- Brachycistidinae:** 12:0>1, 16:0>1, 48:1>2, 106:0>1, 115:0>1, 124:0>1, 137:1>3, 188:1>0
- (Myzininae, Methochinae): 1:0>1, 130:1>0, 164:1>0
- Myzininae:** 2:1>0, 37:1>0, 63:1>2, 71:0>1, 133:0>1, 145:0>1, 162:1>0
- Methochinae:** 11:0>1, 14:0>1, 56:2>1, 80:1>2, 89:0>1, 96:0>1, 110:1>0, 118:2>1, 121:2>1, 129:0>1, 131:0>1, 135:0>1, 137:1>2, 183:0>1, 193:1>3

Table I. Data matrix for Aculeata derived from Rasnitsyn (1980), as in Appendix II. Variables 7, 9, 12-15, 20-21 and 36 are nonadditive. A corrected score is indicated in the Note. A question mark denotes missing data (state unknown in the taxon).

Plumariidae	10111000??	?000000000	0000000010 00000000
Scolecbythidae	101110000?	?000000000	0000000010 00000000
Sclerogibbidae	1012103011	0103000001	0000000010 00000000
Embolemlidae	1021102120	1201100001	0000000010 00000000
Dryinidae	1011102021	1103000001	0000000010 00000000
Bethylidae	1011120000	0011300001	0000000010 00000000
Chrysididae	1011110030	0022200001	0000000010 00000000
Sphecidae	0100001000	0000011012	1000010000 00000100
Apidae	010000104?	0000011012	2000010000 00100000
Tiphidae	0100001000	0010311103	0111101011 11100120
Sapygidae	0200001050	0010011103	0100101111 11100111
Mutillidae	0200001050	0010011103	0111101211 11100111
Sierolomorphidae	00000010??	?010011100	0100101011 11100010
Pompilidae	0100001061	0000011010	3000101111 11100110
Rhopalosomatidae	0100001071	0000011010	3000102011 11101020
Formicidae	0100001081	0010011104	4111102011 11101200
Scoliidae	0100001000	0010311104	0111102011 11112300
Vespidae	0100001001	0010011104	5111102011 11113000
Bradynobaenidae	0100001091	0010311104	0111102011 11100100

Note:

Variable 13 = 0 in Embolemlidae; State I is not general in that taxon.

Table II. Data matrix for Aculeata derived from Rasnitsyn (1988), as in Appendix III. Variables 7, 9, 12-15, 20-21, 23 and 35 are nonadditive. Corrected scores are indicated in the Notes. A question mark denotes missing data (state unknown in the taxon).

Plumariidae	10111000??	?000000000	0000000100	0000000001	00101?0
Scolecbythidae	101110000?	?000000000	0000000100	0000000100	0010100
Sclerogibbidae	1012103011	0103000001	0000000100	0000000112	0010100
Embolemlidae	1021102120	1201100001	0000000100	0000000113	1010100
Dryinidae	1011102021	1103000001	0000000100	0000000110	0010100
Bethylidae	1011120000	0011300001	0000000100	0000000110	1010100
Chrysididae	1011110030	0022200001	0000000100	0000000110	1010100
Sphecidae	0100001000	0000011012	1000100000	0000100000	0110000
Apidae	010000104?	0000011012	2000100000	0100000000	0110000
Tiphidae	0100001000	0010311103	0101010111	1100120000	0110101
Sapygidae	0200001050	0010011103	0101011111	1100011000	0110100
Mutillidae	0200001050	0010011103	0101012111	1100001000	0110101
Sierolomorphidae	00000010??	?010011100	0111010111	1100010000	01111?0
Pompilidae	0100001061	0000010010	3001011111	1100110000	0111000
Rhopalosomatidae	0100001071	0000011010	3001020111	1101020000	0111000
Formicidae	0100001081	0010011104	4111020111	1101200000	0111110
Scoliidae	0100001000	0010311104	0101020111	1112300000	0110101
Vespidae	0100001001	0010010104	5121020111	1113000000	0110110
Bradynobaenidae	0100001091	0010311104	0101020111	1100100000	0110101

Notes:

Variable 13 = 0 in Embolemlidae; State I is not general in that taxon.

Variable 43 = 1 in all, see Brothers (1975: Character 85), Rasnitsyn (1980).

Table III. Data matrix for Aculeata derived from Brothers (1975). The character state trees have been coded using nonredundant linear coding (Appendix IV); spaces separate the variables representing each of the original 92 characters. Where a character is sometimes sexually dimorphic, scoring is as explained in the text. A question mark denotes missing data (state unknown in the taxon, except as explained in the Notes).

Plumariidae	0 1 0 0 00 00 000 0 000 1 0 0 0 0 0000 00 0 00 0 0 000 0 00 01 1 00 0 0 00000 00 00 00 0 00 000 0000 0 10 0 0 0 1 0 0 1 10000 0 0 0 000 01 0 0 00 0 01 100 0 0 00 100 100 00 00 00 0 0 0000 000001 00 00 0 0 0 0 0 0 0 1 1 00 1 0000 00 0 00 ??? ? ? ??? ? ? ?
bethylids	0 0 0 0 00 00 000 0 000 0 0 0 0 0 0000 00 1 00 0 0 000 0 00 00 0 00 0 0 00000 00 00 00 0 00 010 0000 0 00 0 0 0 1 0 0 1 20000 0 0 1 001 01 0 0 00 0 01 000 0 0 00 000 000 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 0 1 0 00 0 0000 00 0 00 000 0 0 0000 0 0
Scolebythidae	0 0 0 0 10 00 001 0 100 0 0 0 0 0 0000 00 0 00 0 1 000 0 00 00 0 01 0 0 00000 00 00 00 0 01 010 0000 0 00 0 0 0 1 0 0 1 30000 0 0 2 002 01 0 0 00 0 01 010 0 0 00 001 001 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 00 0 0000 00 0 00 ??? ? ? ??? ? ? ?
sphecids	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 01 0 0 020 1 01 00 1 10 1 0 00001 00 01 00 1 00 001 0001 0 00 1 0 0 0 0 0 0 00000 1 0 0 000 00 0 0 00 0 00 000 0 0 00 200 200 00 20 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 01 0 0000 00 0 00 000 0 0 1000 0 0
apids	0 0 0 1 00 00 000 0 000 0 0 1 0 0 1000 00 0 01 0 0 010 1 01 00 1 10 1 0 00001 01 01 00 1 00 001 0001 0 00 1 0 0 1 0 0 1 00000 1 0 0 100 10 0 0 00 0 00 000 0 0 00 100 100 10 20 00 0 0 0000 000000 00 00 0 0 0 0 0 0 2 0 0 01 2 0000 01 1 00 010 0 1 2000 0 1
Anthoboscinae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 100 0000 0 10 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 0 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 0 1 0000 10 0 00 000 1 0 0000 0 0

Table III (cont.)

Thynninae	0 1 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 100 0000 0 10 0 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 1 10 100 0 0 00 200 200 00 00 00 1 0 0000 100000 00 00 0 0 0 0 0 0 1 0 0 00 1 0000 00 0 00 000 1 0 0000 0 0
Myzininae	1 0 0 0 00 01 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10000 00 20 00 0 00 200 0000 0 10 0 0 0 0 0 0 0 00000 0 0 0 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 0 0 0000 000000 00 00 0 0 0 0 1 0 1 0 0 00 0 0010 00 0 00 000 1 0 0000 0 0
Methochinae	1 1 0 0 00 01 001 0 010 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 10 0 0 10000 00 10 00 0 00 100 0000 0 10 0 0 0 1 0 0 0 00100 0 0 0 100 01 1 0 00 0 10 000 0 0 00 100 100 00 00 01 0 1 0001 200000 00 00 0 0 0 0 1 0 1 0 0 10 0 0010 00 0 00 000 1 0 0001 0 0
Tiphiinae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 100 1 00 10 1 10 0 0 10000 00 20 00 1 00 200 2000 0 10 0 0 0 2 0 1 1 00010 0 0 1 000 01 1 0 00 0 10 100 0 0 00 200 200 00 00 00 1 0 0000 000000 00 00 1 0 0 0 1 0 1 0 0 10 2 0010 01 1 00 000 1 0 0000 0 0
Brachycistidinae	0 1 0 0 00 00 000 1 000 1 0 1 0 0 0000 00 0 00 0 0 100 1 00 10 1 10 0 0 20000 00 20 00 1 00 100 2000 0 10 0 0 0 1 0 1 1 00000 0 0 1 000 01 1 0 01 0 10 100 0 1 00 200 200 10 00 00 1 0 0000 300000 00 00 1 0 0 0 1 0 1 0 0 10 2 0010 01 1 00 ??? ? ? ???? ? ?
Sapygidae	0 0 0 0 00 10 000 0 000 0 0 1 0 0 0010 00 0 00 0 0 000 0 00 10 1 10 0 0 10010 00 10 00 0 00 100 0000 0 20 0 0 0 0 0 0 0 00000 0 0 0 100 01 1 1 00 1 20 000 0 0 00 200 200 00 00 00 1 0 0000 000000 00 00 0 0 0 0 0 0 1 0 1 00 1 0000 00 0 01 010 0 0 000? 0 0
Myrmosinae	0 1 0 0 00 10 000 0 010 0 0 1 1 1 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 10020 00 10 10 0 00 100 1000 0 20 0 0 0 2 0 0 0 00000 0 0 0 100 01 1 1 10 1 20 000 0 0 00 200 200 00 00 00 2 0 0000 020000 00 10 0 0 0 0 1 0 1 0 0 10 0 0000 01 0 01 000 1 0 0001 0 0

Table III (cont.)

mutillids	0 1 0 0 00 10 000 0 000 0 0 1 1 1 0000 00 0 10 0 0 100 0 00 10 1 10 0 0 10020 10 10 10 0 10 100 1000 0 30 0 0 0 2 0 0 1 00000 0 0 1 100 01 1 1 10 1 20 000 0 0 00 200 200 00 00 00 1 0 0000 011000 10 10 0 0 0 0 1 0 1 0 0 10 1 0000 00 0 01 000 1 0 0001 0 0
Sierolomorphidae	0 0 0 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 0 0 0 10000 00 10 00 0 00 000 0010 0 20 0 0 0 1 0 0 1 01000 0 0 1 100 01 0 0 00 1 01 000 0 0 00 100 100 00 00 00 1 0 0000 000000 00 00 0 0 0 0 0 0 1 0 0 00 0 1000 01 0 00 ??? ? ? ???? ? ?
Pompilidae	0 0 0 0 00 00 000 0 000 0 0 1 0 0 0000 00 0 00 0 0 000 1 00 10 1 10 0 0 10010 00 10 10 1 00 000 0010 0 20 0 0 0 0 0 0 0 00000 1 1 0 100 01 0 0 10 1 10 000 0 0 00 200 200 00 10 00 0 0 1000 000000 00 00 0 0 0 0 0 0 1 0 1 00 1 0000 00 0 00 100 1 0 0010 0 0
Rhopalosomatidae	0 0 0 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 10 0 0 100 1 00 10 1 10 1 0 20000 00 20 10 0 00 000 0010 0 20 0 0 0 0 0 0 1 10000 1 1 1 100 01 0 0 10 0 10 001 0 0 00 100 100 00 00 00 0 0 1000 000000 00 00 1 0 0 0 0 0 1 0 0 01 1 0000 00 0 00 001 0 0 0000 0 0
Formicidae	0 0 1 0 00 00 000 0 100 0 0 1 0 0 0000 00 0 10 0 0 100 1 10 10 1 10 1 0 20100 01 00 00 2 00 200 1000 1 20 0 0 0 0 0 0 0 10000 1 0 0 100 01 0 0 01 1 10 000 0 0 00 300 300 00 00 10 0 0 0010 000000 00 00 1 1 0 0 1 0 1 0 0 01 0 0000 00 0 00 100 0 1 1100 1 0
Scoliidae	0 0 0 0 01 00 010 0 001 0 0 1 0 0 0100 00 0 10 1 0 200 1 10 10 2 10 1 0 21000 10 01 01 1 00 200 1100 0 21 1 0 1 0 0 1 1 00000 1 1 1 000 01 0 0 01 2 10 100 0 1 01 110 110 10 10 00 0 0 0000 000000 00 00 1 0 0 0 1 0 1 0 0 00 0 0100 01 1 10 100 0 0 ?000 0 0
Vespidae	0 0 0 0 01 00 010 0 000 0 0 1 0 0 0100 00 0 10 1 0 300 1 10 10 2 10 1 0 30000 00 01 10 1 00 200 1000 0 20 0 0 0 0 1 0 0 00000 1 1 0 000 01 0 0 01 1 10 000 0 0 00 100 100 00 00 0 0 0100 000000 00 00 0 0 0 0 1 0 1 0 1 00 1 0000 00 1 00 100 0 1 2000 1 0
Eotillini	0 1 0 1 00 00 000 0 100 1 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 00000 01 00 00 1 00 200 0010 0 00 1 1 0 1 0 0 1 00000 0 0 1 100 01 0 0 10 0 10 000 1 0 00 100 100 00 00 00 1 0 0000 000200 01 01 1 1 1 0 1 0 1 0 ? 01 1 0000 00 0 00 ??? ? ? ???? ? ?

Table III (cont.)

Typhoctini	0 1 0 1 00 00 000 0 100 1 0 1 0 0 0000 00 0 00 0 0 000 0 00 10 1 10 0 0 20000 01 00 00 1 00 200 0010 0 00 1 1 0 1 0 0 1 00000 1 0 1 000 01 0 0 10 2 01 000 0 0 00 200 200 00 00 00 1 0 0000 000200 01 01 1 1 1 0 1 0 1 0 1 01 1 0000 00 0 00 ??? ? ? ??? ? ? ?
Chyphotinae	0 1 0 0 00 10 100 1 000 1 0 1 1 0 0000 00 0 00 0 0 000 1 10 10 1 10 0 0 20000 01 00 00 2 00 200 1000 0 00 1 1 0 1 0 0 1 00000 0 0 1 100 01 0 0 10 2 10 100 0 0 00 200 300 00 00 00 0 0 0000 000110 01 01 1 1 2 2 1 0 1 0 1 01 1 0001 10 0 00 ??? ? ? ??? ? ? ?
Apterogyninae	0 1 0 0 00 10 100 1 001 1 1 1 1 0 0000 00 0 00 0 0 000 1 10 10 1 10 0 1 20000 01 00 00 1 10 200 1000 0 00 1 2 0 1 0 0 2 00001 2 0 2 000 01 0 0 01 2 10 100 1 0 10 300 300 00 11 00 1 0 0000 000110 01 00 2 1 2 1 1 1 1 0 0 01 1 0001 00 1 00 ??? ? ? ??? ? ? ?
Bradynobaeninae	0 1 0 0 00 11 100 0 001 1 1 1 1 0 0001 01 1 00 0 0 001 1 10 10 1 10 0 2 20000 01 00 00 1 10 200 2000 0 00 1 2 0 1 1 1 2 00002 2 0 2 010 01 0 0 01 2 10 100 1 1 20 400 400 01 13 00 0 0 0000 000110 02 00 1 1 2 1 1 0 1 0 1 10 1 0002 00 1 00 ??? ? ? ??? ? ? ?

Notes:

Sapygidae:

Character 90 (Variables 157 - 160), uncertainty as to whether female closes off cavity containing prey.

Scoliidae:

Character 90 (Variables 157 - 160), uncertainty about transport of prey.

Bradynobaeninae:

Variables 7 & 8 coded to indicate derivation of 8:1 from 7:1.

Table IV (cont.)

Table IV. Data matrix for final analysis of Aculeata using characters of Appendix VI. Variables 32, 53, 57, 80, 81, 89, 90, 100, 133, 143, 144, 147, 154, 178, 190, 204, 205, 208 and 218 are nonadditive. Comments on changes in scoring from those in Table III (from Brothers, 1975) appear in the Notes. Scores for other taxa and variables not included in Table III are taken from later authors or they are newly scored, as indicated in the Notes and Appendix VI. A question mark (?) denotes missing data (state unknown in the taxon); a dash (-) denotes a taxon for which the variable is inapplicable.

Plumariidae	0100000000	0000010000	0000000010	0010000000	1010000000	0000000000
	0000000000	0000000001	1001100000	0000000000	0200000010	1000000100
	1000000000	0000000000	0010000000	0100000011	1001000000	0000????00
	00?0010000	0030011100	000?010000	00021?????		
Bethylidae	0000010000	1000000000	1100000010	0000000000	0010000000	0000010000
	0002010000	0000100002	1011200000	0000200100	22- -000010	1000000000
	0000000000	0000010000	0000000000	0102000001	0000000000	0000100000
	0000030000	1030010100	1010011110	100012010		
Chrysididae	0000000000	1100000000	0000001010	0000000000	0000000100	0001000000
	0002010000	0000000002	1001210000	0000100100	12- -000010	1000000000
	0000000000	0000010000	0000000000	0103001001	0001000001	1000100000
	0000030000	1000010100	1013011200	000011000		
Sclerogibbidae	0100000100	0020000010	1000000010	0010000001	1011000000	0010010000
	0001010000	0010000000	2001201000	0010200101	03- -000010	2001000000
	0000000000	0000010000	0001000000	0100000101	1001000000	0000101000
	0000030000	1030010100	1101012300	00021?????		
Dryinidae	0000000000	0010000001	0000000011	0000000100	0000010000	0000000000
	0001010000	0000000000	2001220000	0000100110	03- -000010	1000000000
	0001000000	0000010000	0000000000	0100000001	0002000001	1000101000
	0000030000	1030020100	1102111300	000012010		
Embolemidae	0000000000	0010000001	0000011010	0200000101	0011000000	0020012000
	2001020000	0000000000	1001210000	0010100110	03- -000010	1000100000
	0000000000	0000010000	0002000000	0100000001	0002000001	1000100000
	0000030000	1030021100	1102121100	011112000		

Table IV (cont.)

Scolebythidae	0000000000	1010000000	0000000000	0010000000	0100100000	0000000000
	0000000000	0000000001	1001200000	0000200200	02- - 000010	1000000001
	0010000000	000000- - -	- - - -000000	0100000001	0000000000	0000????00
	0000020000	1020010100	1000011000	00001????		
sphecids	0000000000	0000000100	0000000000	0000101010	0011000000	0100002000
	1000110001	0000001001	0000000000	0010000000	0000000000	0000000200
	2000020000	000000- - -	- - - -000000	0000010000	0010000000	0000000001
	0000001000	0100001101	1008000000	0000000000		
Heterogynaidae	0100000000	0000000100	0000000000	0000100010	0011010000	0100002000
	1000110001	0000001001	2001000002	0010110000	0200000010	0000100200
	2000010001	0020000000	0020000000	0000010000	?010000000	1000????0?
	???0000010	0120001100	100??00000			
apids	0001000000	0000000100	0010000000	0000101020	0011010000	0100102000
	1000111001	0000001001	0001000000	0010010000	0200000000	0000000100
	1001020000	0000000000	0000000000	0000020000	0012000001	10000100-2
	0000101000	0100021100	100-000300	0000000000		
Anthoboscinae	0000000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	0010000000	0000000000	0000000000	0110000101	0000000200
	2000000000	000000- - -	- - - -000000	0000010000	0001000010	0000000100
	0000002000	0001001120	1000000000	0000000000		
Thynninae	0100001000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	1011000001	0000000000	0000000000	0110001101	0000000200
	2000000001	0000001000	0000000000	0001020000	0101000000	0001000100
	0000002000	0011001120	1000000000	0001000000		
Diamminae	0100000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	1011000001	0000000000	0000000000	0110001101	0000000200
	2000000001	0000001100	0000000000	0001010000	0001000000	0000????01
	0000002000	0011001120	1004000000	00000????		

Table IV (cont.)

Myzininae	1000001000	0000000100	0000000000	0000000001	0011000100	0000020000
	0020000000	1011000001	1000000000	0000000000	0210000101	0000000200
	2000000000	0010001000	0000100000	0001010000	0000001000	0000000100
	0000002100	0011101120	1000000000	0002000000		
Methochinae	1100001000	1001000100	0000000000	0000001001	0011000100	0000010000
	0010000000	0011000002	1000000010	0000000000	0210000100	0000000100
	1000000010	1000102000	0000000000	0001010000	0100001000	0000000100
	0010002100	0031101120	1000000000	0002000000		
Tiphinae	0000000000	0000000100	0000000000	0001001001	0011000100	0000020000
	1020010000	0012000001	1011000001	0000100000	0210000101	0000000200
	2000000001	000000- - -	- - - -000010	0001010000	0102001001	1000000100
	0000002100	0011101120	1000000000	0002000000		
Brachycistidinae	0100000000	0100010100	0000000000	0001001001	0011000200	0000020000
	1010010000	0011000001	1011000000	0000100000	0210010101	0000100200
	2001000001	0000003000	0000000010	0001010000	0102001001	1000????00
	00?0002000	0011101120	100?000000	00020????		
Fedtschenkiinae	0000010000	0000000100	1020000000	0000000001	0011000100	1000010000
	0010010000	0010000001	1000000000	0000010000	02-1001200	0000000200
	2000010001	000000- - -	- - - -000000	0004010000	1001000000	0010????00
	00?0002000	0011001110	1005?00000	00000????		
Sapyginae	0000010001	0000000100	1010100000	0000000001	0011000100	1000010000
	0010000000	0010000000	0000000000	0000010000	02-1001200	0000000000
	0000000001	000000- - -	- - - -000000	0000010000	1102000000	1010010000
	0000002000	0011001101	1005000000	000000010		
Myrmosinae	0100010000	0001000100	1100000000	0000000001	0011000100	2000011100
	0010010000	0010000000	2000000000	0000010000	02-1101200	0000000200
	2000000002	0000000020	0000001000	0001010000	0100000001	0010000100
	0010002000	0031101110	1005000000	0001000000		

Table IV (cont.)

mutillids	0100010000	0000000100	1100000001	0001000001	0011000100	2001011100
	0110010000	0020000001	2001000000	0000110000	0200101200	0000000200
	2000000001	0000000011	0000101000	0001010000	0101000000	0010000100
	0010002000	0031101110	1005000000	0002000000		
Sierolomorphidae	0000000000	0010000100	0000000000	0000001001	0011000100	0000010000
	0000010100	0010000001	1001000100	0000110000	0200001010	0000000100
	1000000001	0000000000	0000000000	0000010000	0000100001	0000???00
	00?0002001	0021001101	100?000000	00000???		
Pompilidae	0000000000	0000000100	0000000000	0000001001	0011000100	1000010100
	1000010100	0010000000	0000000000	0002010000	0200101100	0000000200
	2000010000	0100000000	0000000000	0000010000	1002000000	0000100101
	0100001000	0010001110	1006000000	000100100		
rhopalosomatids	0000000001	0010000100	0000000001	0000001101	0011010200	0000020100
	0000010201	0010000000	0000000000	0112110000	0200100100	0100000100
	1000000000	010000- - -	- - - -000010	0000010000	0011000000	0000001000
	0000002002	0010101101	1007200000	0000000001		
<i>Olixon</i>	0000000000	0010000100	0000000001	0010000001	0011010201	0000120100
	10100- - -	- 010000002	1010000000	0222110002	02- - - - - 0	0100000000
	0000000000	0200000000	0000002010	0000010000	0011000000	0000???00
	00000- - -	-- 10101101	1007200001	0000-???		
Formicidae	0010000000	0010000100	0000000001	0001001201	0011010201	0000101000
	2020010000	0110000000	0000100000	0010010000	0200111100	0000000300
	3000000100	0001000000	0003000011	0001010000	0010000000	0000100011
	1001003000	0031101100	100?000000	0002000000		
Scoliinae	0000100001	0000100100	0001000001	1002001201	0021010210	0001011010
	1020011010	0000011010	0011000000	0012100000	0200112101	0000102110
	1101010000	000000- - -	- - - -000010	0001010000	0000020001	1100100002
	0000002003	0011101120	1000000000	000000120		

Table IV (cont.)

Proscoliinae	0000000000	0000100100	0000001001	1002001101	0011010210	0001011010
	1020000000	0000010011	1011000020	0011100000	0200112101	0000101110
	1100010000	000000- - - -	- - - -000010	0000010000	0000010010	1100??????
	?????02003	0011001120	1000000000	00000????		
Vespidae	0000100001	0000000100	0001000001	0103001201	0021010300	0000001100
	1020010000	0010000000	0100000000	0012000000	0200111100	0000100100
	1000000000	001000- - - -	- - - -000000	0001010000	1001000000	1000100012
	0001002003	0001201100	1000000000	000000100		
Eotillini	0101000000	0010010100	0000000000	0000000001	0011000200	0000101000
	1020000000	1000101102	0001000000	0000110000	0200100100	0010000100
	1000000001	0000000000	2000010111	100101000?	?011000000	0000????00
	00?00?????	??31101110	100??00000	00010????		
Typhoctini	0101000000	0010010100	0000000000	0000000001	0011000200	0000101000
	1020000000	0000101102	0001000000	0010100000	0200102110	0000000200
	2000000001	0000000000	2000010111	1001010000	1011000000	0000100200
	0000002100	0031101110	1009000000	00010?0?0		
Chyphotinae	0100010010	0100010100	1000000000	0000001101	0011000200	0000101000
	2020000000	0000101102	1001000000	0000110000	0200102101	0000000200
	3000000000	0000000000	1100010111	2021010000	1011000110	0000????00
	00?0002000	0031201110	100??00000	00010????		
Apterogyninae	0100010010	0100111100	1000000000	0000001101	0011001200	0000101000
	1120010000	0000101202	0002000000	1020200000	0200112101	0010010300
	3000011001	0000000000	1100010021	2011110000	0011000100	1000????00
	00?0002000	0011201110	100??00000	00010????		
Bradynobaeninae	0100011010	0000111100	1000010110	0000011101	0011002200	0000101001
	1120010000	0000101202	0112000000	2020201000	0200112101	0010120400
	4000112000	0000000000	1100020011	2011010000	1101000200	1000????00
	00?0003000	0031101110				
	100??00000	0001-????				

Table IV (cont.)

Notes:

- Variable 7: Thynninae & Methochinae see Kimsey (1991); doubtfully correct (see above discussion of her paper).
- Variable 10: Myzininae, Kimsey (1991) corrected.
- Variable 11, 13: Scelebythidae corrected based on *Ycaploca*.
- Variables 19-20: newly scored.
- Variable 21: Fedtschenkiinae, Sapyginae, Brothers (1975) corrected.
- Variables 23, 25: newly scored.
- Variable 27: Sclerogibbidae, Embolemidae, Carpenter (1986) corrected.
- Variable 29: Plumariidae see Carpenter (1986), Brothers (1975) corrected.
- Variables 31, 32: newly scored.
- Variable 33: newly scored; Plumariidae, Scelebythidae, Brothers (1975) corrected.
- Variable 34: rhopalosomatids corrected based on *Liosphex*.
- Variable 35: sphecids corrected based on Dolichurini.
- Variables 38, 39, 41, 42: newly scored.
- Variable 43: Bethylidae, Sclerogibbidae, Embolemidae, Carpenter (1986) corrected.
- Variable 46: sphecids corrected based on Dolichurini.
- Variable 53: newly scored.
- Variable 56: Scoliinae, Brothers (1975) corrected.
- Variables 57, 59: newly scored.
- Variable 60: newly scored; Bradynobaeninae, Brothers (1975) corrected.
- Variable 64: newly scored; Carpenter (1986) corrected.
- Variables 66-71: newly scored; Brothers (1975) corrected.
- Variables 73-76: newly scored; Brothers (1975) corrected.
- Variables 80, 81: newly scored.
- Variable 84: rhopalosomatids corrected based on *Liosphex*.
- Variable 85: Scelebythidae see Carpenter (1986); *Olixon* postulated condition from which State 1 of Variable 92 derived.
- Variables 87, 89, 90, 92: newly scored.
- Variable 93: Pompilidae see Rasnitsyn (1980).
- Variable 94: newly scored.
- Variable 96: *Olixon* postulated condition from which State 2 of Variable 98 derived.
- Variables 98-102: newly scored; Brothers (1975) and Carpenter (1986) corrected.
- Variables 103, 104: mutillids, Myrmosinae, Brothers (1975) corrected.
- Variable 105: Formicidae, Scoliinae, Proscoliinae, Vespidae, Apterogyninae, Bradynobaeninae postulated condition from which State 1 of Variable 106 derived in these taxa.
- Variable 108: Typhoctini postulated condition from which State 1 of Variable 109 derived.
- Variables 110-112, 114: newly scored.
- Variable 115: Vespidae see Carpenter (1981).
- Variable 117: newly scored.
- Variable 124: Embolemidae corrected, see Carpenter (1990a).
- Variables 131-138, 143, 144, 147, 152, 154, 157-159: newly scored, and Brothers (1975) corrected.
- Variable 161: Bethylidae, Chrysididae, Sclerogibbidae, Dryinidae, Embolemidae see Rasnitsyn (1980); Thynninae, *Olixon*, Proscoliinae newly scored; also see Quicke, Fitton & Ingram (1992).
- Variable 164: Pompilidae, Brothers (1975) corrected.
- Variables 166, 174: newly scored.
- Variables 175-177: Bethylidae, Chrysididae, Dryinidae, Sclerogibbidae (derived state of Variable 175 assumed as precursor to derived state of Variable 177) see Evans (1987) and Stefani (1956); Embolemidae see Wharton (1989); Typhoctini unpublished information.
- Variable 178: newly scored; Typhoctini unpublished information.

Table IV (cont.)

- Variable 179: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to provision with more than one prey.
- Variable 180: Diamminae, Scolinae see Clausen (1940).
- Variables 180-183: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous females highly unlikely to relocate prey but Heterogynaidae (see Day 1984) may do so.
- Variable 184: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to oviposit before prey located.
- Variable 185: Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Typhoctini unpublished information; Plumariidae, Heterogynaidae, Sierolomorphidae (some females apterous, unpublished), Brachycistidinae, Eotillini, Chyphotinae, Apterogyninae and Bradynobaeninae apterous or brachypterous females highly unlikely to provision with plant material.
- Variables 186-193: newly scored.
- Variable 194: scored following Rasnitsyn (1980, 1988).
- Variables 195-197: newly scored.
- Variable 198: scored following Brothers (1975) and Rasnitsyn (1980) (not Rasnitsyn 1988).
- Variables 199-202: newly scored.
- Variable 203: newly scored, and see Carpenter (1986) and Rasnitsyn (1988).
- Variable 204: newly scored; Scolebythidae see Evans, Kugler & Brown (1980) and Brothers (1981); Chrysididae see Kimsey & Bohart (1990); Diamminae see Clausen (1940); sphecids see Iwata (1976); Typhoctini unpublished information; and see Carpenter (1986) and Rasnitsyn (1980, 1988).
- Variable 205: newly scored; Dryinidae see Olmi (1984); Embolemidae see Wharton (1989); rhopalosomatids, *Olixon* see Townes (1977); and see Carpenter (1986).
- Variables 206, 207: scored following Rasnitsyn (1980, 1988).
- Variables 208-216: newly scored.
- Variables 217-219: newly scored and see Evans (1987), Stefani (1956), Wharton (1989); Typhoctini unpublished information.

TableV. Data matrix for ground plans of families of Vespoidea other than those included as such in Table IV, using characters of Appendix VI. The ground-plan state of each variable is the relatively most plesiomorphic state found in any of the component taxa of the family, or the known state where states are unknown in some component taxa, unless otherwise specified in the Notes. Variables 32, 53, 57, 80, 81, 89, 90, 100, 133, 143, 144, 147, 154, 178, 190, 204, 205, 208 and 218 are nonadditive. A question mark (?) denotes missing data (state unknown in the taxon); a dash (-) denotes a taxon for which the variable is inapplicable.

Tiphiidae	0000000000	0000000100	0000000000	0000000001	0011000100	0000020000
	0010000000	0010000000	0000000000	0000000000	0110000101	0000000200
	2000000000	000000- - - -	-000000	0000010000	0001000010	0000000100
	0000002000	0001001120	1000000000	0000000000		
Sapygidae	0000010000	0000000100	1010000000	0000000001	0011000100	1000010000
	0010000000	0010000000	0000000000	0000010000	02-1001200	0000000100
	1000000001	000000- - - -	-000000	0000010000	1001000000	0010010000
	0000002000	0011001110	1005000000	000000010		
Mutillidae	0100010000	0000000100	1100000000	0000000001	0011000100	2000011100
	0010010000	0010000000	2000000000	0000010000	0200101200	0000000200
	2000000001	0000000010	0000001000	0001010000	0100000000	0010000100
	0010002000	0031101110	1005000000	000100000		
Rhopalosomatidae	0000000000	0010000100	0000000001	0000000001	0011010200	0000020100
	0000010201	0010000000	0000000000	0111110000	0200100100	0100000100
	1000000000	010000- - - -	-000010	0000010000	0011000000	0000001000
	0000002002	0010101101	1007200000	0000000001		
Scoliidae	0000000000	0000100100	0000000001	1002001101	0011010210	0001011010
	1020000000	0000010010	0011000000	0011100000	0200112101	0000101110
	1100010000	000000- - - -	-000010	0000010000	0000010000	1100100002
	0000002003	0011001120	1000000000	000000120		
Bradynobaenidae	0100000000	0000010100	0000000000	0000000001	0011000200	0000101000
	1020000000	0000101102	0001000000	0000100000	0200101100	0000000100
	1000000000	0000000000	1000010011	1001010000	0011000000	0000100200
	0000002000	0021101110	1009000000	00010?0?0		

Notes:

Tiphiidae: Variables 56, 110, 118, 121: states in Methochinae considered reversals.

Sapygidae: Variables 118, 121: ground plan states considered intermediate between states in subfamilies. Variable 199: state in Sapyginae considered reversal.

Rhopalosomatidae: Variables 118, 121: states in *Olixon* considered reversals.

Bradynobaenidae: Variable 107: ground-plan state considered intermediate between states in components. Variable 163: state in Bradynobaeninae considered reversal. Variable 193: ground-plan state considered intermediate between states in components.

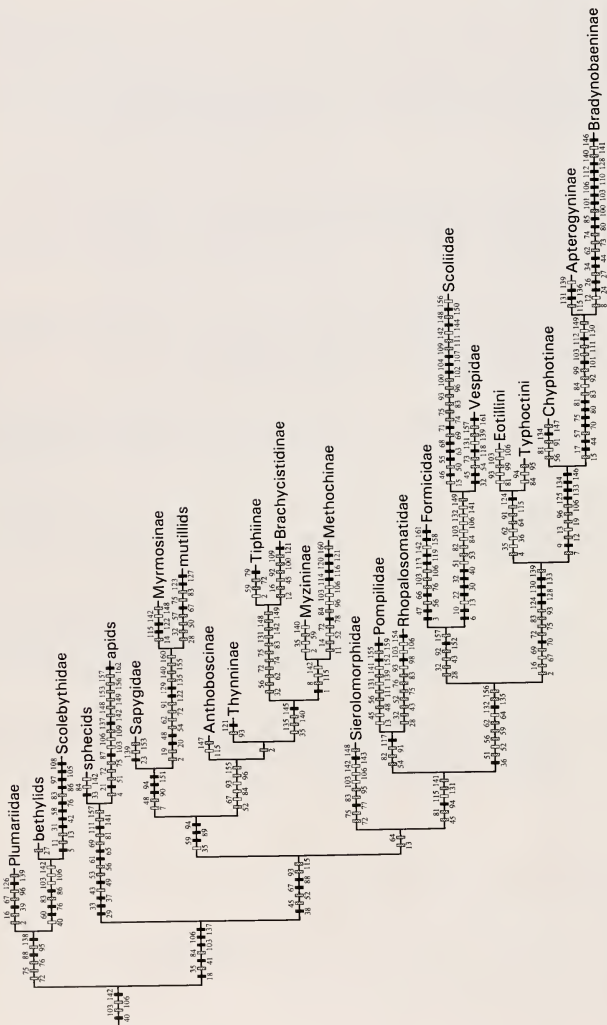


Fig. 1. Cladogram of Aculeata from Brothers (1975: Fig. 2), with distribution of variables based on scoring in Table III plotted using accelerated transformation option of Clados (Nixon 1992), except using delayed transformation for variables considered unlikely to show reversals (length 408, consistency index 0.51, retention index 0.62); state changes determined by Brothers (1975) and those plotted by Clados (translated into codes originally used by Brothers) given in in

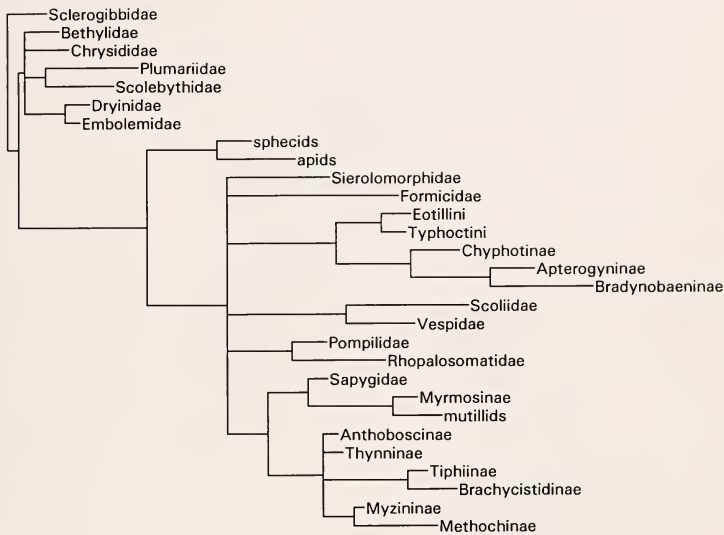


Fig. 2. Phylogeny of Aculeata after Königsman (1978: Figs. 4, 13).

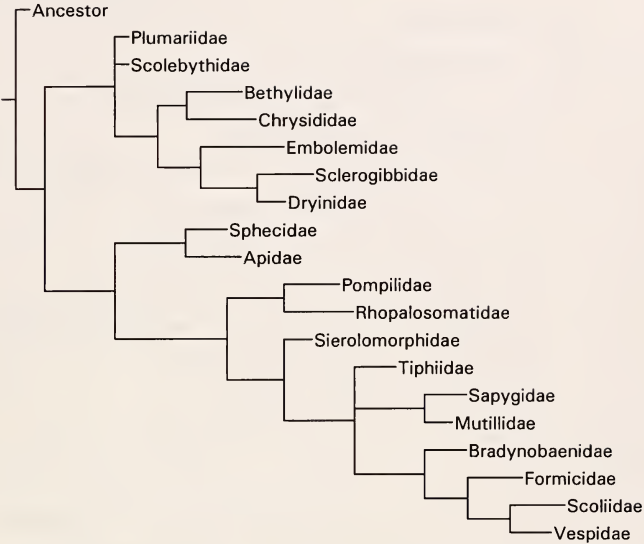


Fig. 4. Strict consensus tree for three cladograms of Aculeata based on characters and states from Rasnitsyn (1980) (as coded in Appendix II and scored in Table I) resulting from exact analysis by implicit enumeration (length 94, consistency index 0.76, retention index 0.88) and stable to successive approximations character weighting as implemented in Hennig86.

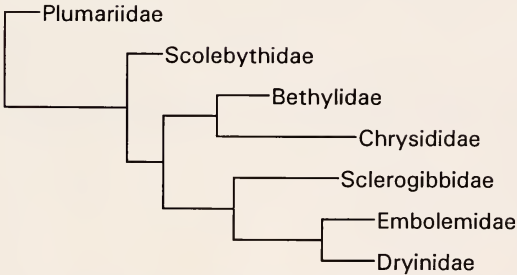


Fig. 5. Cladogram of Chrysidoidea from Carpenter (1986: Fig. 4).

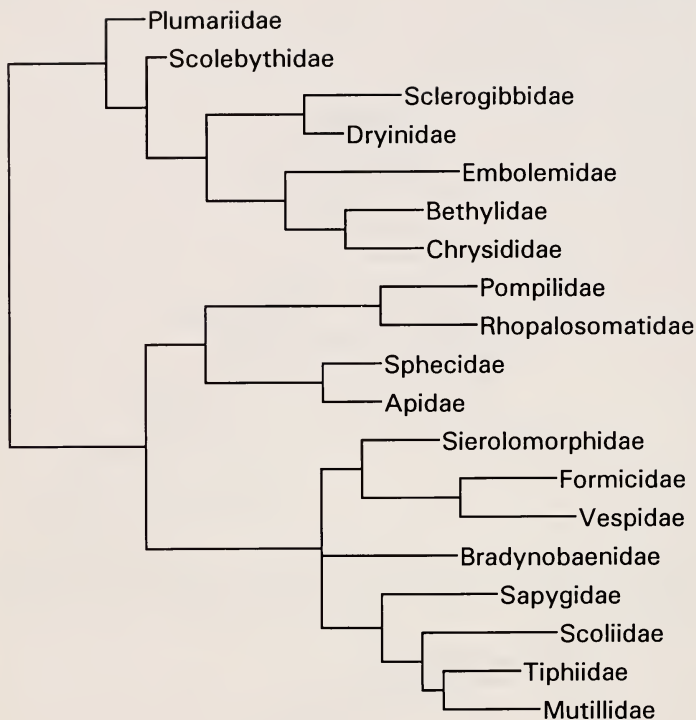


Fig. 6. Phylogeny of Aculeata from Rasnitsyn (1988: Fig. 4); ambiguous position of Bradynobaenidae indicated as a trifurcation (length 132, consistency index 0.63, retention index 0.78 based on scoring in Table II).

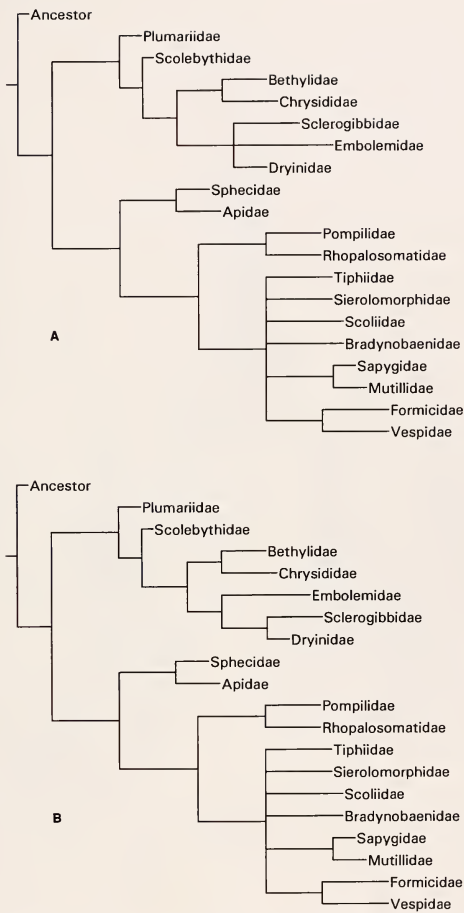
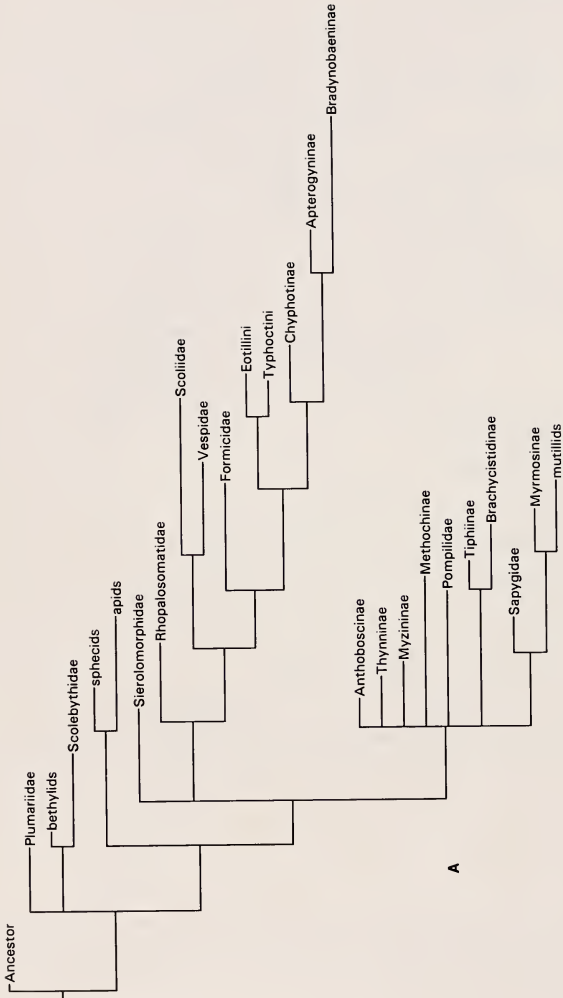


Fig. 7. Results of analysis of characters and states for Aculeata from Rasnitsyn (1988), as coded in Appendix III and scored in Table II. 7a. Strict consensus tree for six cladograms resulting from exact analysis by implicit enumeration (length 118, consistency index 0.71, retention index 0.84). 7b. Strict consensus tree for two cladograms resulting from successive approximations character weighting (weighted length 684); these two cladograms are among the initial six.



A

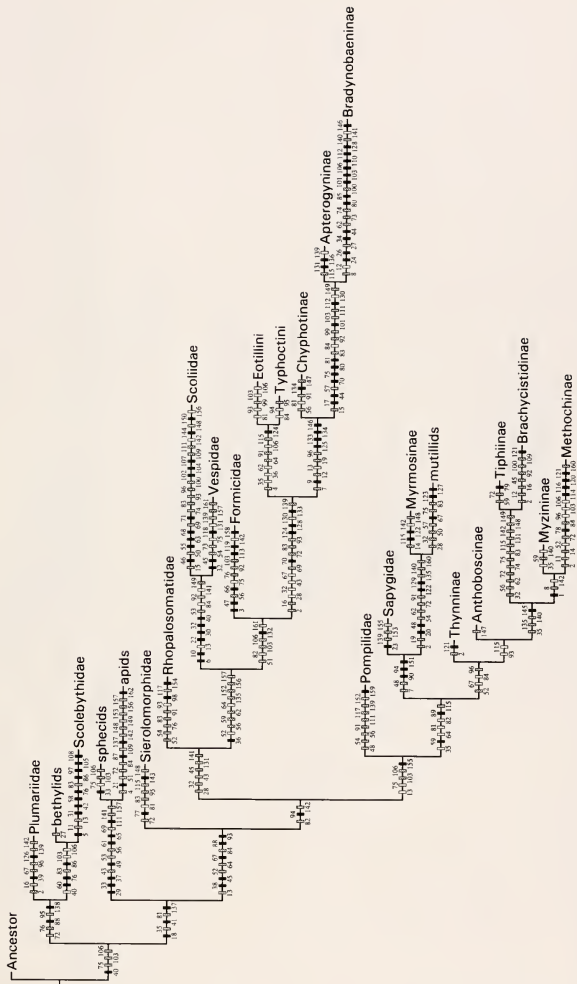
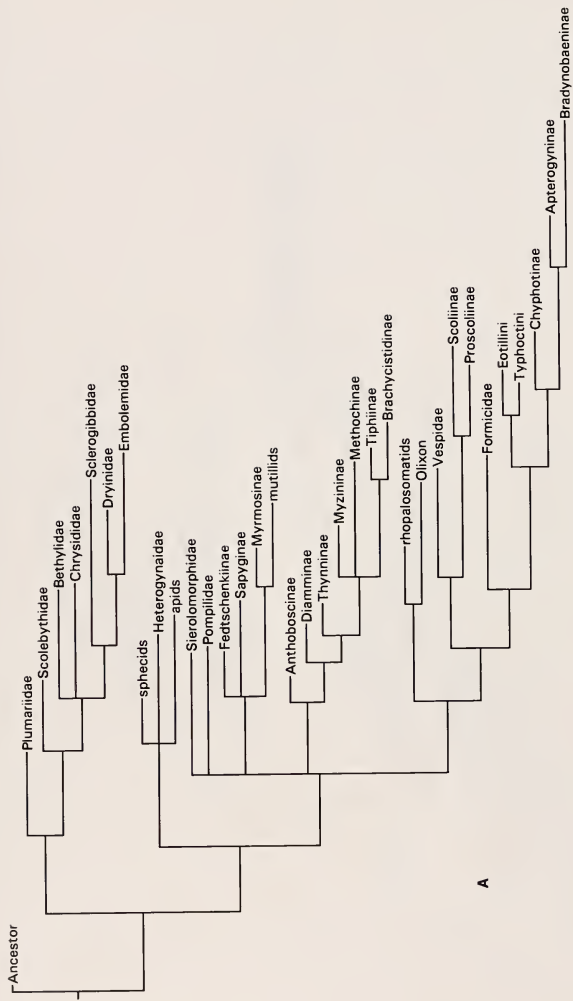


Fig. 8. Results of analysis of characters and states for 25 taxa of Aculeata from Brothers (1975), as coded in Appendix IV and scored in Table III. 8a. Strict consensus tree for eight cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 401, consistency index 0.52, retention index 0.64). 8b. Preferred cladogram (see text) of two produced by successive approximations character weighting (both are among the initial eight; weighted length 1463); state changes given in Appendix V. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal



A

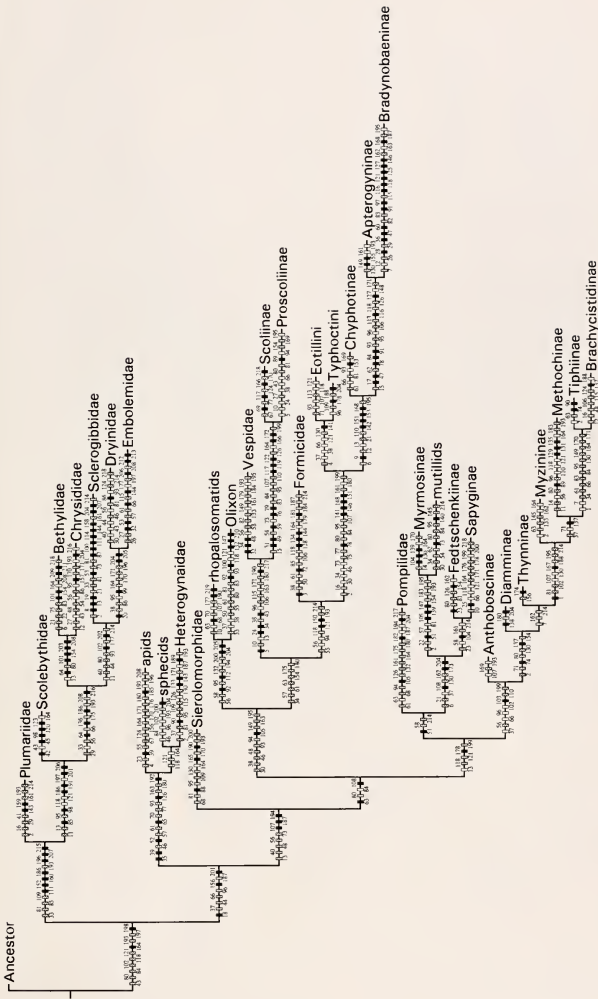
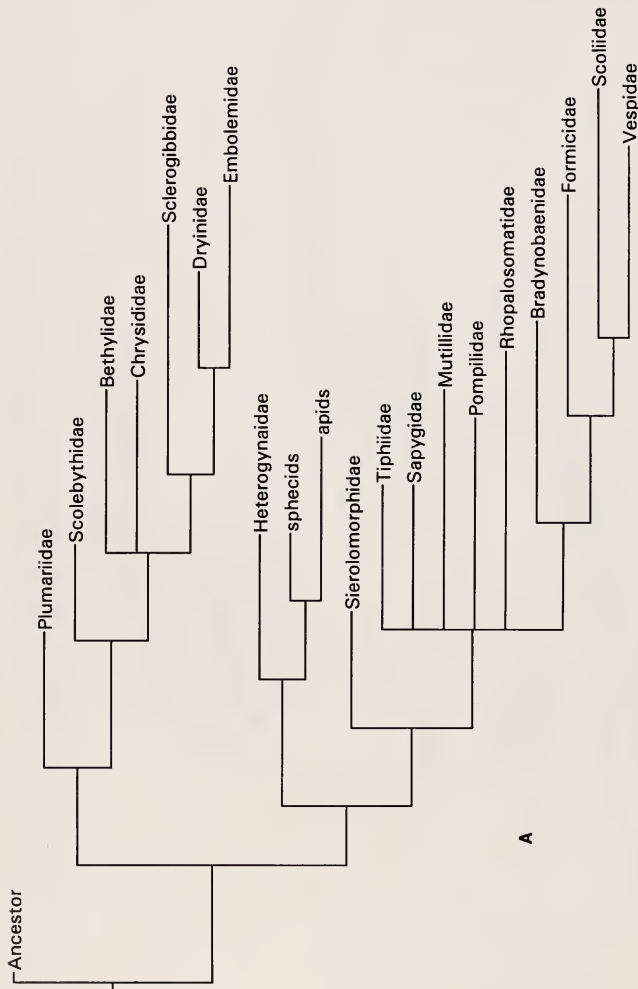


Fig. 9. Results of analysis of characters and states for 34 taxa of Aculeata, as coded in Appendix VI and scored in Table IV. 9a. Strict consensus tree for 64 cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 689, consistency index 0.46, retention index 0.66). 9b. Preferred cladogram (see text) of two produced by successive approximations character weighting (only this one is among the initial 64; weighted length 2173); state changes given in Appendix VII. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).



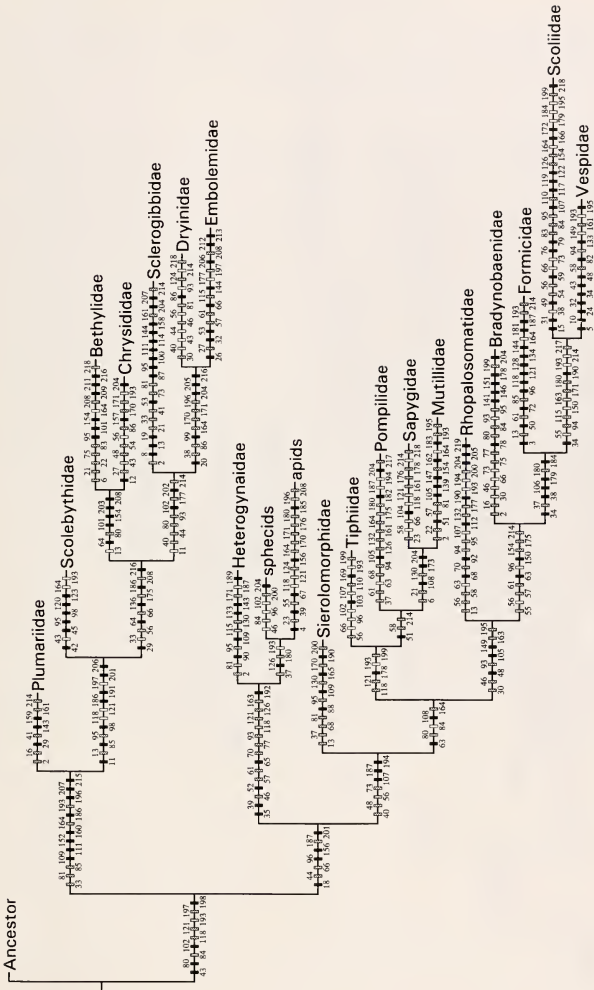


Fig. 10. Results of analysis of characters and states for 20 family groundplans of Aculeata, as coded in Appendix VI and scored in Tables IV and V. 10a. Strict consensus tree for four cladograms resulting from approximate analysis by multiple tree searching with extended branch swapping (length 467, consistency index 0.54, retention index 0.63). 10b. Preferred cladogram (see text) of two produced by successive approximations character weighting (only this one is among the initial four; weighted length 1701); state changes given in Appendix VIII. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

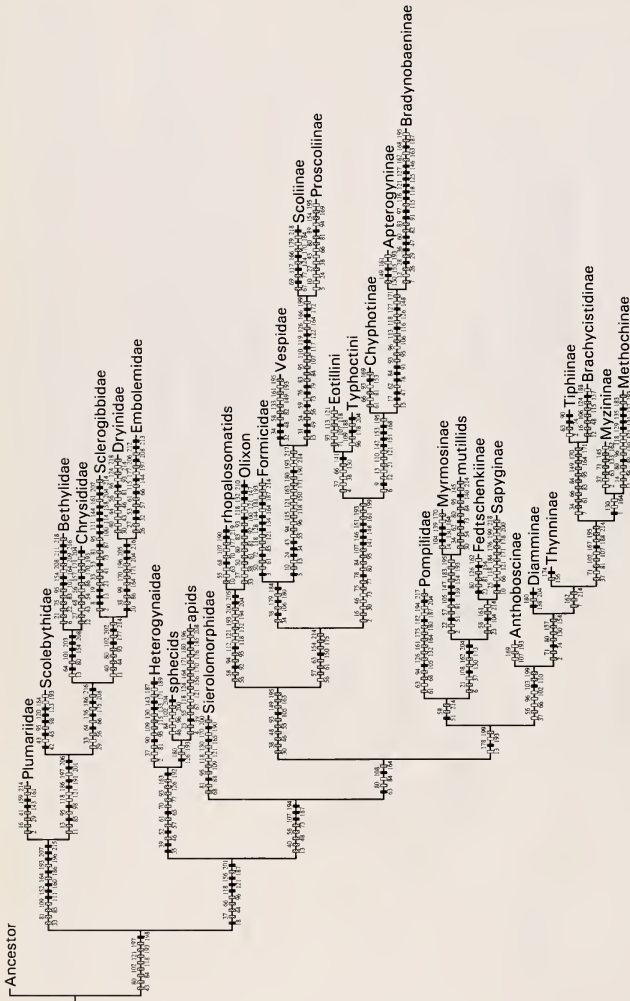


Fig. 11. Composite cladogram based on preferred results (see text) of all analyses of Aculeata (length 692, consistency index 0.46, retention index 0.65); state changes given in Appendix IX. Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

SCIENTIFIC NOTE

On *Odynerus rachiphorus* Schletterer, a Masarinae (*Trimeria*), not a Eumeninae (Hymenoptera, Vespidae)

Schletterer (1891) described five species of *Odynerus*, all supposedly from Chile. Thanks to the kindness of M. Fischer from the Vienna Museum, we were able to study a male specimen labeled *Odynerus rachiphorus* in Schletterer's handwriting. The specimen was not labeled as a type and it was sent to us as a non-type specimen.

A careful comparison of the specimen and Schletterer's original description shows that he had in front of him a Masarinae (*Trimeria*) and not a Eumeninae (*Odynerus*) when he described *rachiphorus*. The scutellum, the insertion of the antennae close to the eye margins, the lateral processes of the propodeum punctuate, bearing an apical spine, and the pattern of sculpture of the metasomal terga are descriptive features that prove this and indicate that the Vienna specimen is the holotype. It is interesting to note that it bears a second label "*Trimeria rachiphorus*" written by Kohl. The species should then bear the name *Trimeria rachiphorus* (Schletterer) **new combination**.

The holotype corresponds to a species of *Trimeria* broadly distributed in Argentina and previously known as *Trimeria buyssoni* Bréthes (1904) (Willink 1951; Richards 1962). Bréthes' name is thus a junior synonym of *Trimeria rachiphorus* (Schletterer), **new synonymy**. The species has

been recorded from the Provinces of Jujuy, Salta, Tucuman, Formosa, Santiago del Estero, Santa Fe, Catamarca and Neuquen in Argentina and also from Paraguay. It has never been found in Chile and we suggest the Schletterer's specimen is mislabeled. The holotype of *Odynerus rhodopterus*, together with *Odynerus fairmairei*, are two more species described by Schletterer from Chile that have never been found in that country.

LITERATURE CITED

- Bréthes, J. 1904. *Trimeria buyssoni* un nuevo masarido argentino. *Anales del Museo Nacional de Buenos Aires* (3)2:371-374.
- Richards, O. W. 1962. *A revisional study of the masarid wasps (Hymenoptera, Vespoidea)*. British Museum (Natural History), London. 294 pp.
- Schletterer, A. 1891. Vespidarum species novae chilensis. *Entomologische Nachrichten* 17(6):83-94.
- Willink, A. 1951. Una nueva especie argentina de *Trimeria* (Hym., Masaridae). *Revista de la Sociedad entomologica Argentina* 15:77-82.
- A. Willink. Instituto Miguel Lillo, Miguel Lillo 205, 4000 Tucuman, Argentina and A. Roig Alsina. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. A. Gallardo 470, 1405 Buenos Aires, Argentina.

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